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Comparative Myology of Moles and the Phylogeny of the Talpidae (Mammalia, Lipotyphla)

HOWARD P. WHIDDEN[1]

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[1] Assistant Professor, Department of Biology, Augustana College, Rock Island, IL 61201; Research Associate, Division of Vertebrate Zoology, American Museum of Natural History.

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ABSTRACT

The skeletal musculature of 11 talpid genera is described, and 58 myological characters are defined and used in a phylogenetic analysis of the Talpidae. This analysis included the outgroup taxa *Atelerix* (Erinaceidae) and *Blarina* (Soricidae), and it discovered a single most parsimonious tree. Inclusion of *Uropsilus* in a monophyletic Talpidae needs further evaluation, but there is very strong support for the monophyly of other talpids. Contrary to previous interpretations of talpid relationships, this phylogenetic analysis indicates (1) the fully fossorial moles *Parascalops*, *Scalopus*, *Scapanus*, and *Talpa* are monophyletic; (2) the Eurasian genus *Talpa* is sister taxon to the North American genera *Scalopus* and *Scapanus*; and (3) the long-tailed mole *Scaptonyx* is part of a clade with the shrew moles *Neurotrichus* and *Urotrichus*. Preliminary biogeographic analysis suggests that the Talpidae originated in the Old World, and that there were separate dispersals from Eurasia to North America by *Condylura*, *Neurotrichus*, *Parascalops*, and the common ancestor of *Scalopus* and *Scapanus*.

INTRODUCTION

The mammalian family Talpidae contains the fossorial moles, the shrew moles, and the desmans. The Talpidae has traditionally been classified in the order Insectivora (e.g., Simpson, 1945; Hutterer, 1993), although changing views on mammalian phylogeny and classification have led some recent workers to place it either in the order Lipotyphla (e.g., Butler, 1972, 1988; MacPhee and Novacek, 1993) or the order Erinaceomorpha (e.g., McKenna and Bell, 1997). There is disagreement as to the sister group of talpids, with some workers holding that it is the Erinaceidae (McDowell, 1958; Van Valen, 1967; McKenna and Bell, 1997) and others that it is the Soricidae (Butler, 1988; Carroll, 1988). Although it is generally agreed that talpids form a monophyletic lineage (Yates and Moore, 1990), there have been no explicit statements of derived characters for the group. Recent classifications of the Talpidae (Van Valen, 1967; Yates, 1984; Corbet and Hill, 1991; Hutterer, 1993; McKenna and Bell, 1997) have recognized between 12 and 17 genera and between 31 and 42 species. In the present study I follow the classification of Corbet and Hill (1991), which recognized 12 genera and 31 species (table 1).

Living talpids exhibit a remarkable diversity of lifestyles and locomotor habits, which Yates and Moore (1990) categorized as ambulatory, semifossorial, semiaquatic, aquatic/fossorial, and fossorial (table 1). The Chinese shrew moles (*Uropsilus*) have well-developed ear pinnae and unspecialized forefeet (Nowak, 1991), and their locomotor habits are probably best described as ambulatory. The American and Japanese shrew moles (*Neurotrichus* and *Urotrichus*, respectively) have reduced ear pinnae, thickened palms, and heavy claws. They will burrow at least occasionally (Nowak, 1991), and can be considered semifossorial. The habits of the long-tailed mole (*Scaptonyx*) have apparently not been recorded (Nowak, 1991), but this mole is similar in external form to *Neurotrichus* and *Urotrichus*, and it is probably also semifossorial. The desmans (*Desmana* and *Galemys*) are semiaquatic, with webbed feet and a tail that is laterally compressed for at least part of its length (Nowak, 1991). The star-nosed mole (*Condylura*) is an accomplished burrower, with broadened forefeet and heavy claws. However, it also swims regularly in fresh water, and Yates and Moore (1990) considered it to be aquatic/fossorial. The remaining genera (*Parascalops*, *Scalopus*, *Scapanulus*, *Scapanus*, and *Talpa*) are the New and Old World burrowing moles, and they can be considered fully fossorial.

The oldest fossils assigned to the Talpidae are from the late Eocene of Europe (McKenna and Bell, 1997). In contrast, talpids do not appear in North America until the late Oligocene (McKenna and Bell, 1997). This time difference suggests a Eurasian origin for the group, with subsequent dispersal to North America. However, it is not clear when moles arrived in North America, how many invasions there were, or what route(s) they took. Dobson (1891) believed that the New World fossorial moles are derived from an Old World ancestor similar to *Talpa* that

TABLE 1
Classification of the Talpidae
Classification, common names, and geographic distributions after Corbet and Hill (1991), with number of recognized species in parentheses. Locomotor habits after Yates and Moore (1990).

Taxa	Common name	Geographic distribution	Locomotor habits
Subfamily Uropsilinae			
Uropsilus (3)	Chinese shrew moles	China and Burma	Ambulatory
Subfamily Desmaninae			
Desmana (1)	Russian desman	Russia and Siberia	Semiaquatic
Galemys (1)	Pyrenean desman	France, Portugal, and Spain	Semiaquatic
Subfamily Talpinae			
Talpa (15)	Eurasian moles	Eurasia	Fossorial
Scaptonyx (1)	Long-tailed mole	China and Burma	Semifossorial
Neurotrichus (1)	American shrew mole	Western North America	Semifossorial
Urotrichus (2)	Japanese shrew moles	Japan	Semifossorial
Scapanulus (1)	Kansu mole	China	Fossorial
Parascalops (1)	Hairy-tailed mole	Eastern North America	Fossorial
Scapanus (3)	Western American moles	Western North America	Fossorial
Scalopus (1)	Eastern American mole	Eastern and central North America	Fossorial
Condylura (1)	Star-nosed mole	Eastern North America	Aquatic/fossorial

crossed a Bering land bridge, and that the American shrew mole *Neurotrichus* is the result of a second invasion by a form similar to the Japanese shrew mole *Urotrichus*. Hutchison (1976) contended that only ambulatory moles could have crossed a Bering land bridge, implying the independent development of full fossoriality in the New and Old World fossorial moles. Vaughan (1986) held that the Talpidae reached North America across a North Atlantic bridge in the early Tertiary, but he did not comment on the number of dispersal events. Moore (1986) argued for three separate invasions of North America: one for the New World burrowing moles (*Parascalops*, *Scalopus*, and *Scapanus*), one for *Condylura*, and another for *Neurotrichus*.

Recent phylogenetic hypotheses for the Talpidae have been based on osteology (Hutchison, 1968, 1976), allozymes (Yates and Greenbaum, 1982; Moore, 1986), and a combination of genic, cytogenetic, and morphological characters (Yates and Moore, 1990). However, these previous studies have not included data matrices, and only Moore (1986) provided an explicit discussion of characters and character polarities. In addition, only Hutchison (1976) and Yates and Moore (1990) included all extant genera. The phylogenies of Hutchison (1976) and Yates and Moore (1990) differ in important ways, but they both separate the fully fossorial Old World genus *Talpa* from the fully fossorial New World genera *Parascalops*, *Scalopus*, and *Scapanus* (fig. 1). This implies either that full fossoriality evolved independently in *Talpa* and the North American fossorial moles, or that some taxa secondarily lost fossorial habits. Also, both phylogenies separate *Scaptonyx* from *Neurotrichus* and *Urotrichus*, which implies that the similarity in external form between *Scaptonyx* and the two shrew moles is due either to primitive features or to convergence.

Comparative myology has been a valuable source of characters for systematic analyses of mammals (e.g., Klingener, 1964; Woods, 1972; Griffiths, 1982; Dunlap et al., 1985; Stein, 1986, 1990; Ryan, 1989). Although intergeneric variation in myology has been noted in talpids (Dobson, 1882–1890; Campbell, 1939; Reed, 1951), myological characters have never been used for the phylogenetic analysis of the group. In the present study I use comparative myology as a new source of characters for the phylogenetic analysis of the Talpidae. I describe the skeletal musculature of 11 talpid genera, define muscle differences between taxa as characters, and use these characters in the first true cladistic analysis of talpid phylogeny. I then compare the clades discovered in this anal-

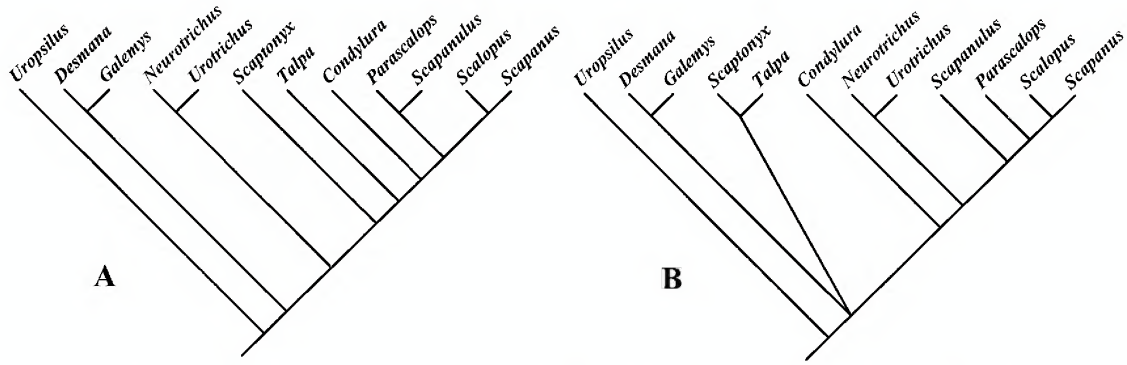

Fig. 1. Two recent phylogenetic hypotheses for the Talpidae, modified to include only extant taxa and to conform to the generic classification of Corbet and Hill (1991). **A**, Hutchison (1976:13), based on osteology; **B**, Yates and Moore (1990:15), based on morphology, genetics, and cytogenetics.

ysis with those recognized in previous phylogenies, addressing three specific questions: (1) Did full fossoriality evolve independently in the New and Old World burrowing moles, or are the fully fossorial moles monophyletic? (2) Is the similarity between *Scaptonyx*, *Neurotrichus*, and *Urotrichus* due to primitive features or convergence, or are these semifossorial taxa monophyletic? (3) How many dispersal events were involved in the origin of the Recent North American mole fauna?

SPECIMENS EXAMINED

I dissected 37 fluid-preserved talpid specimens (table 2), including 11 of the 12 genera recognized by Corbet and Hill (1991). The only genus that I was not able to dissect is *Scapanulus*, which is very rare in study collections (Nowak, 1991). I assumed that the polytypic genera *Scapanus*, *Talpa*, and *Urotrichus* are monophyletic, and since previous myological studies of mammals have found little myological variation below the generic level (Rinker and Hooper, 1950; Rinker, 1963; Stein, 1986), I considered *Scapanus townsendii*, *Talpa europaea*, and *Urotrichus talpoides* as representative of their respective genera. I also assumed that *Uropsilus* is monophyletic, and I let *U. gracilis* and *U. soricipes* represent this genus.

I dissected the entire skeletal muscular system with the exception of the extrinsic ocular muscles, the diaphragm, the perineum, and most of the intrinsic muscles of the back. Also, I did not dissect in detail the muscles associated with the ear pinna of *Uropsilus* because the other study taxa do not have pinna muscles. Several of the specimens available to me were not intact, and therefore I was not able to describe all muscles for all taxa; notable gaps are in the cranial muscles of *Galemys* and in the upper pelvic limb muscles of *Scaptonyx*. Furthermore, fluid-preserved specimens of *Desmana*, *Galemys*, *Scaptonyx*, *Uropsilus*, and *Urotrichus* are rare in museum collections, and in these I did not dissect the deeper axial muscles. These muscles showed little variation in the other taxa, and their dissection would have caused considerable damage to the specimens.

Dissections were made under a Bausch and Lomb Stereozoom Microscope (3.5–30×) and a Nikon SMZ-U Stereoscopic Microscope (3.75–37.5×). Dermal muscles were dissected by first shaving the fur and vibrissae from the head and neck region, and then gradually shaving and peeling away the sequential layers of facial muscles. An iodine stain (Bock and Shear, 1972) was used to identify the fiber direction of the smallest and thinnest muscle layers.

Muscle descriptions include information on origin, insertion, shape, and topographic position relative to other anatomical structures. Nongenetic factors such as mode of preservation and the size, age, and condition of the specimens at the time of preservation may all contribute to apparent variation in myology (Stein, 1986; personal obs.), and

TABLE 2
List of Specimens Examined

Abbreviations: AMNH, American Museum of Natural History; HPW, personal collection of the author; TTU, Texas Tech University; UMA, University of Massachusetts Museum of Zoology; UMMZ, University of Michigan Museum of Zoology; USNM, United States National Museum, Smithsonian Institution. Arranged by family, and then alphabetically by genus and specimen number.

Talpidae	
Condylura cristata	
HPW 339	USA, Massachusetts, Franklin Cty.
HPW 359	USA, Massachusetts, Franklin Cty.
HPW 377	USA, Massachusetts, Franklin Cty.
UMA 3216	USA, Massachusetts, Hampshire Cty.
UMA 3217	USA, Massachusetts, Hampshire Cty.
Desmana moschata	
AMNH 244222	Russia, Vladimir Region, Murom
Galemys pyrenaicus	
HPW 400	No collection data available
USNM 152522	France, Ariege Dèpartement, Ax-les-Thermes
Neurotrichus gibbsii	
HPW 327	USA, Washington, Kings Cty.
HPW 328	USA, Washington, Kings Cty.
TTU 29909	USA, Washington, Pierce Cty.
UMA 3916	Canada, British Columbia, Vancouver
Parascalops breweri	
HPW 298	USA, Massachusetts, Hampshire Cty.
HPW 299	USA, Massachusetts, Franklin Cty.
HPW 341	USA, Massachusetts, Franklin Cty.
HPW 360	USA, New York, Columbia Cty.
HPW 371	USA, Massachusetts, Hampden Cty.
HPW 387	USA, Massachusetts, Hampshire Cty.
TTU 29914	USA, Ohio, Ashtabula Cty.
UMA 3157	USA, Massachusetts, Hampshire Cty.
Scalopus aquaticus	
HPW 350	USA, Massachusetts, Hampshire Cty.
HPW 362	USA, Massachusetts, Hampshire Cty.
HPW 363	USA, Massachusetts, Hampshire Cty.
TTU 29957	USA, Michigan, Clinton Cty.
Talpidae *(continued)*	
Scapanus townsendii	
HPW 351	USA, Washington, Kings Cty.
HPW 352	USA, Washington, Kings Cty.
HPW 353	USA, Washington, Kings Cty.
HPW 354	USA, Washington, Kings Cty.
Scaptonyx fusicaudus	
USNM 574391	China, Sichuan, Shimian Xian
Talpa europaea	
UMMZ 62242	Europe
UMMZ 138459	Europe
UMMZ 157792	Europe
Uropsilus gracilis	
AMNH 114565	Burma, Kachin Province
AMNH 232373	China, Szechuan Province
Uropsilus soricipes	
USNM 574389	China, Sichuan, Shimian Xian
Urotrichus talpoides	
AMNH 232456	Japan, Shizuoka Province
USNM 355922	Japan, Shizuoka Province
Erinaceidae	
Atelerix spp.	
HPW 401	No collection data available
HWP 402	No collection data available
Soricidae	
Blarina brevicauda	
HPW 178	USA, Massachusetts, Hampshire Cty.
HPW 357	USA, Massachusetts, Hampshire Cty.
HPW 358	USA, Massachusetts, Franklin Cty.
HPW 369	USA, Massachusetts, Hampshire Cty.

therefore I was conservative in identifying muscle differences between taxa. I did not attempt to make precise size comparisons, although I remark on obvious differences in muscle size between taxa. Muscle innervations were determined only where homology was in question.

The muscle descriptions are arranged into groups according to innervation and topographic position. The myology of *Parascalops* is used as a standard for comparison in the descriptions, and conditions in the other genera are discussed under Remarks. I follow Dobson (1882–1890), Campbell (1939), Reed (1951), Gaughran (1954), and Meinertz (1978a) for muscle nomenclature; where these authorities disagree I note synonyms under Remarks. Problems of homology are also discussed under Remarks. I follow Reed (1951) and Gaughran (1954) in naming osteological structures that serve as points of origin and insertion for muscles. The orientation of the talpid humerus varies considerably in the different genera, and in the fully fossorial genera it is abducted to such a degree that its distal end is dorsal to the glenoid

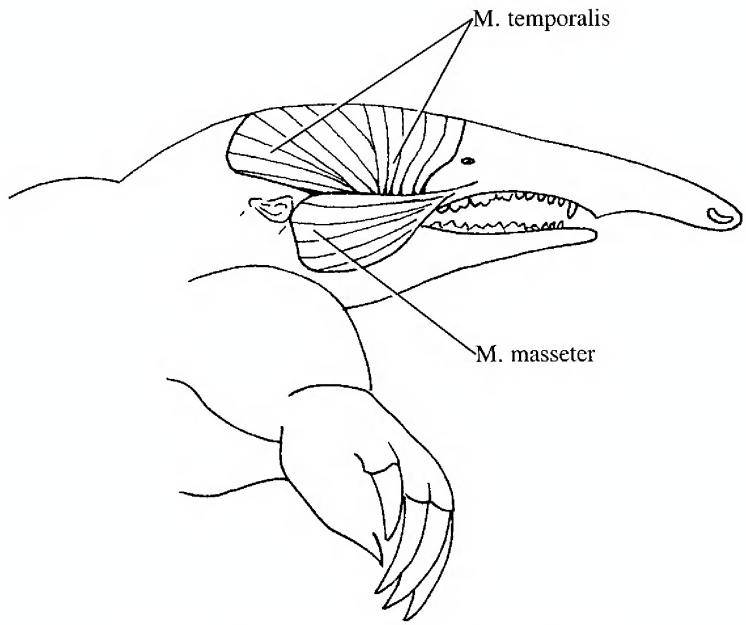

Fig. 2. Masticatory muscles of *Parascalops*.

articulation. Therefore, its anatomically medial surface is actually lateral in position. However, to avoid confusion I use the terms medial and lateral in the muscle descriptions as if the humerus were oriented in the normal quadrupedal position.

Most muscles are illustrated with line drawings of the condition in *Parascalops*, but the intrinsic muscles of the manus are illustrated for *Galemys* and the intrinsic muscles of the pes for *Neurotrichus*. The drawings were prepared with the aid of a camera lucida attachment for the Nikon SMZ-U Stereoscopic Microscope, and they are not to the same scale. They are grouped after the muscle descriptions.

DESCRIPTIVE MYOLOGY

Branchiomeric Musculature

Trigeminal Field

Masticatory Group

M. temporalis (fig. 2)

Origin: From a broad area of the dorsal and lateral skull, extending from the frontal almost to the occipital, and medially to the dorsal midline; some deeper fibers originate from the lateral wall of the skull and from the medial surface of the zygomatic arch.

Insertion: The insertion of this muscle is complex. The anterior fibers extend ventrally to insert on the tip and anterior margin of the coronoid process. The deep anterior fibers from the side of the skull insert on the medial surface of the coronoid process. The dorsal fibers from the midline of the skull converge to a stout insertion on the tip of the coronoid process, with some fibers running onto the medial surface. The posteriormost fibers extend anteriorly to insert along the posterior margin of the coronoid process. The fibers from the medial surface of the zygomatic arch extend anteriorly, then curve ventrally to insert on the anterior margin of the coronoid process.

Remarks: This muscle has the same general form in *Condylura*, *Desmana*, *Neurotrichus*, *Parascalops*, *Scalopus*, *Scapanus*, *Scaptonyx*, *Talpa*, *Uropsilus*, and *Urotrichus*. In *Uropsilus*, the portion from the medial surface of the zygomatic arch is particularly well developed.

M. masseter (figs. 2, 6, and 7)

Origin: A superficial layer from the maxillary root and the lateral surface of the an-

terior zygomatic arch, and a deep layer from the ventral surface of the posterior zygomatic arch.

INSERTION: The superficial portion on the lateral surface and posterior and ventral margins of the angular process, the deep portion in the masseteric fossa and along the ventral margin of the condylar process of the dentary.

REMARKS: This muscle has the same general form in the 11 study taxa. The superficial masseter of *Uropsilus* originates from a prominent tubercle at the maxillary root of the zygoma, as Hutchison (1968) suspected. Fiedler (1953) considered the deep layer to be a separate muscle, M. zygomaticomandibularis. Zlabek (1938) provided a detailed description of this muscle for *Talpa* and *Galemys* (his *Myogale*), and Gaughran (1954) compared a number of published descriptions of the talpid masseter.

M. pterygoideus externus

ORIGIN: As a dorsal head from the ventral margin of the frontal bone and a ventral head from the orbitotemporal region.

INSERTION: The fibers of the two heads converge and attach on the medial surface of the condylar process of the mandible.

REMARKS: This muscle has the same general form in *Condylura*, *Desmana*, *Galemys*, *Neurotrichus*, *Parascalops*, *Scalopus*, *Scapanus*, and *Talpa*.

Internal Pterygoid Group

M. pterygoideus internus

ORIGIN: From an extensive area dorsal and lateral to the pterygoid region.

INSERTION: Over the entire medial surface of the angular process of the mandible.

REMARKS: This muscle has the same general form in *Condylura*, *Desmana*, *Galemys*, *Neurotrichus*, *Parascalops*, *Scalopus*, *Scapanus*, *Scaptonyx*, *Talpa*, and *Urotrichus*.

M. tensor veli palatini

ORIGIN: From the ventral surface of the skull, just anteromedial to the tympanic ring.

INSERTION: Via an aponeurotic sheet on the posterior surface of the secondary palate.

REMARKS: This muscle has the same general form in *Condylura*, *Desmana*, *Galemys*, *Neurotrichus*, *Parascalops*, *Scalopus*, *Scapanus*, *Scaptonyx*, *Talpa*, and *Urotrichus*. Some fibers of this muscle may insert on the dorsal surface of the pterygoid hamulus; these fibers are especially obvious in *Condylura*. The tendon of insertion of this muscle extends over the pterygoid hamulus, and the belly of the muscle covers the eustachian tube.

M. tensor tympani

I did not find this muscle in the taxa examined.

Mylohyoid Group

M. digastricus, venter anterior (fig. 6)

The posterior portion of the digastric is discussed with the muscles of the Facial Field.

ORIGIN: A lateral portion from a chevron-shaped tendinous inscription with the posterior belly of the digastric, and a medial portion from a tough, concave fascial sheet. This fascial sheet extends posterolaterally from the midline to join the tendinous inscription between the anterior and posterior digastric bellies.

INSERTION: The lateral portion onto the ventral surface of the mandible via a stout digastric tendon, the medial portion onto the ventral surface of the mandible and the digastric tendon.

REMARKS: This muscle has the same general form in *Condylura*, *Neurotrichus*, *Parascalops*, *Scalopus*, *Scapanus*, *Scaptonyx*, *Talpa*, and *Urotrichus*. *Uropsilus* has no medial portion to the anterior belly. *Desmana* has a lateral portion similar to the other taxa, but the medial portion becomes split, with a superficial layer originating from the tendon of the opposite side, and a deep layer originating from the median raphe of M. mylohyoideus profundus; both layers insert on the digastric tendon near its attachment to the mandible. I did not discern the azygous component that Dobson (1882–1890) described for *Desmana*. Gaughran (1954) did not identify a tendinous inscription in this muscle in *Scalopus*, and he identified the lateral portion of the venter anterior as part of the venter posterior. Fiedler's (1953) interpretation of this muscle in *Talpa* is similar to mine.

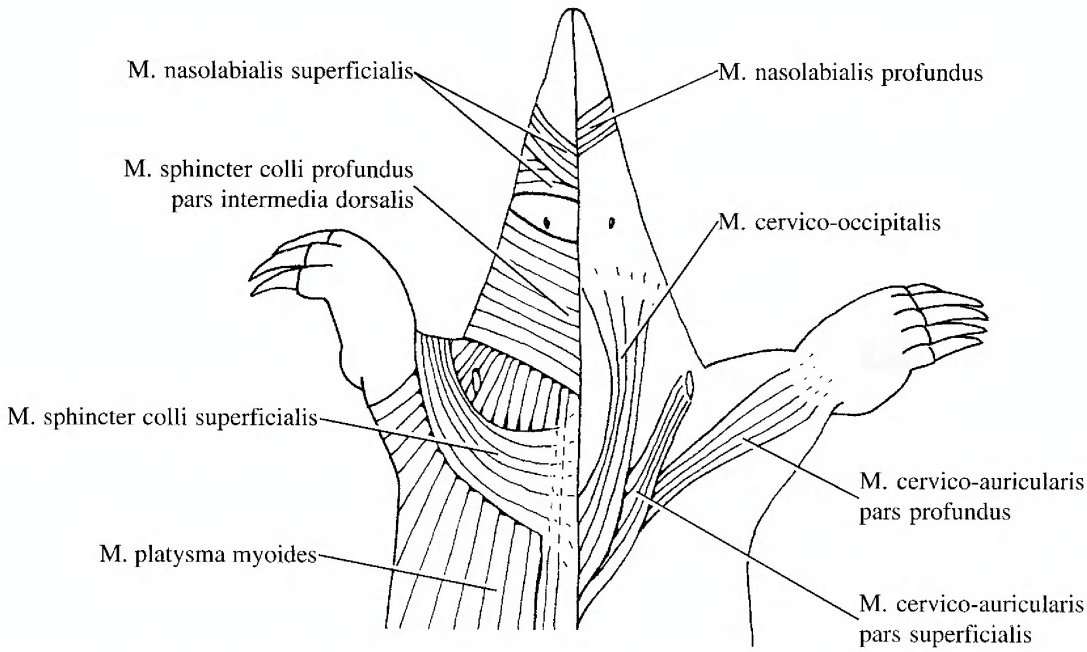

Fig. 3. Dorsal view of facial muscles of *Parascalops*; superficial muscles on left, deeper muscles on right.

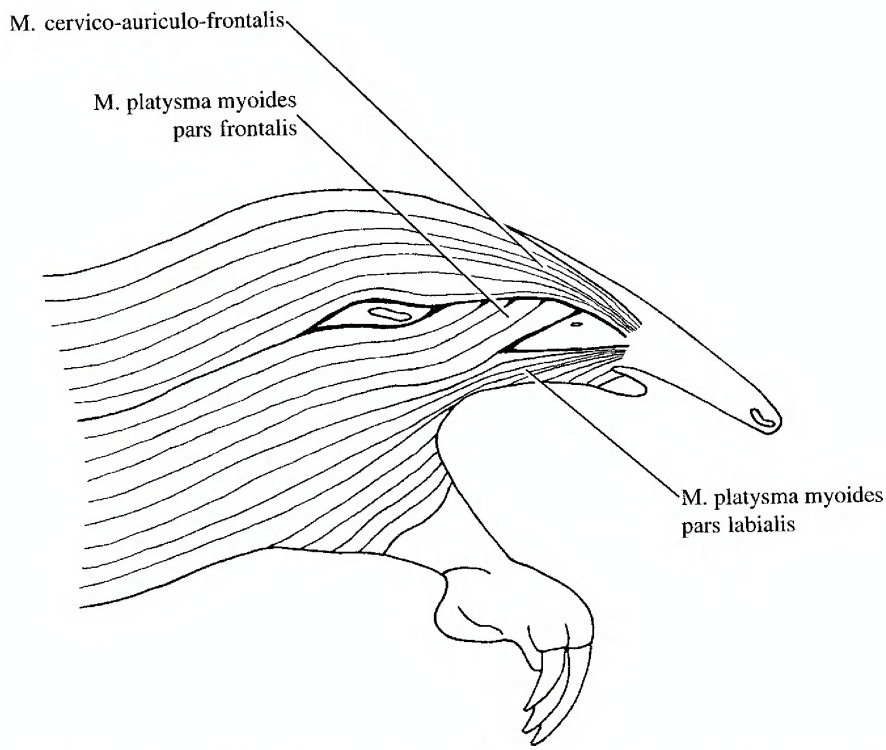

Fig. 4. Lateral view of facial muscles of *Parascalops*, M. sphincter colli superficialis removed.

M. mylohyoideus, pars superficialis (fig. 6)

This muscle is a sheet of transverse fibers that runs between the two halves of the mandible, attaching to the ventral surface of each ramus; there is no indication of a median raphe. This muscle lies deep to M. digastricus and superficial to M. geniohyoideus.

REMARKS: This muscle has the same general form in the 11 study taxa.

M. mylohyoideus, pars profundus

ORIGIN: From the medial surface of the mandible. The anterior fibers extend transversely, whereas the more posterior fibers extend posteromedially.

INSERTION: In a midventral raphe with fibers of the antimere, with the posteriormost fibers attaching to the basihyal cartilage.

REMARKS: This muscle has the same general form in the 11 study taxa. The midventral raphe of this muscle is firmly attached to M. geniohyoideus.

FACIAL FIELD

The muscles supplied by the facial nerve are typically split into two groups, the superficial facial muscles, or muscles of expression, and the hyoid constrictor muscles. The superficial facial muscles of therian mammals consist of three distinct layers: M. sphincter colli superficialis, M. platysma, and M. sphincter colli profundus (Huber, 1930, 1931). M. sphincter colli superficialis is the most superficial of these and has transverse fibers, M. platysma is the middle layer and has longitudinal fibers, and M. sphincter colli profundus is the deepest layer and has transverse fibers. According to Huber, M. sphincter colli superficialis forms at most a simple band encircling the neck, whereas Mm. platysma and sphincter colli profundus give rise to a diversity of specialized facial muscles. I interpret the facial muscles of talpids in this way, and follow Huber's classification in my treatment of these muscles. Meinertz (1978a & 1978b) described in detail the facial muscles of *Erinaceus*, *Talpa*, *Suncus* (his *Pachyura*), and *Sorex*. Although I disagree with some of his interpretations, I have followed his names for these muscles except where noted. *Uropsilus* has a well-developed ear pinna, with a number of associated muscles not found in other talpids; these muscles are not described here.

Superficial Facial Group

M. sphincter colli superficialis (fig. 3)

ORIGIN: From the skin and connective tissue of the ventral midline, where the antimeres decussate.

INSERTION: On the side of the neck and on the dorsal surface of the shoulder. Fibers of M. sphincter colli superficialis appear to merge with fibers of the pars intermedia dorsalis of M. sphincter colli profundus where the two layers overlap.

REMARKS: This muscle has the same general form in *Condylura*, *Desmana*, *Neurotrichus*, *Parascalops*, *Scalopus*, *Scapanus*, *Scaptonyx*, *Talpa*, *Uropsilus*, and *Urotrichus*.

M. platysma and derivatives

The platysmal layer consists of the prominent M. platysma myoides and the various retroauricular muscles. M. cervico-auriculo-frontalis (figs. 2 and 3) is a prominent retroauricular muscle that originates from the dorsal surface of the neck, continuous with and medial to M. platysma myoides. M. mandibulo-auricularis, which extends along the auditory tube, also belongs in this group (Huber and Hughson, 1926). The remaining retroauricular muscles are deeper and originate from the dorsal midline. They are thin, delicate muscles that insert into the skin of the head, neck, and shoulder. In some mammal groups an M. platysma cervicale encircles the neck, but I did not find this muscle in talpids.

M. platysma myoides (figs. 3 and 4)

ORIGIN: In two parts: a large dorsal sheet, which splits to form a pars frontalis and a pars labialis superioris, and a smaller ventral sheet, the pars labialis inferioris. The dorsal platysmal sheet originates with M. cervico-auriculo-frontalis over a broad area of the back and shoulder region, superficial to M. cutaneus maximus. Some fibers also arise from the dorsal surface of the forelimb. Just posterior to the ear opening, this sheet separates from M. cervico-auriculo-frontalis to run ventral to the ear. Anterior to the ear, it

splits to form the pars frontalis and the pars labialis superioris. The pars labialis inferioris originates separately from the posterior and ventral surfaces of the forelimb.

INSERTION: Pars frontalis on the bony rostrum anterior to the eye and deep to M. cervico-auriculo-frontalis, pars labialis superioris into the corner of the mouth, and pars labialis inferioris into the intermandibular fascia, along the angle of the jaw, and in fascia on the side of the head.

REMARKS: The general form of this muscle, with a pars frontalis, pars labialis superioris, and pars labialis inferioris, is similar in *Condylura*, *Desmana*, *Neurotrichus*, *Parascalops*, *Scalopus*, *Scapanus*, *Scaptonyx*, *Talpa*, *Uropsilus*, and *Urotrichus*.

M. cervico-auriculo-frontalis (fig. 4)

ORIGIN: From the skin over the shoulders and back, together with M. platysma myoides pars dorsalis.

INSERTION: On the rostrum just anterior to the eye, superficial to M. platysma myoides pars frontalis.

REMARKS: This muscle has the same general form in *Condylura*, *Desmana*, *Neurotrichus*, *Parascalops*, *Scalopus*, *Scapanus*, *Scaptonyx*, *Talpa*, *Uropsilus*, and *Urotrichus*. This muscle separates from the platysmal sheet to pass dorsal to the ear. It covers the top of the head, where it is continuous at the midline with its antimere. Some fibers from this sheet attach to the skin around the dorsal rim of the ear opening. Dobson (1882–1890) grouped Mm. cervico-auriculo-frontalis and platysma myoides pars frontalis as M. frontocuticularis.

M. interscutularis

The interscutularis is a thin band of fibers extending across the dorsal midline and connecting the dorsal surfaces of the auditory canals. It lies deep to the other facial muscles and superficial to M. temporalis. I found this muscle in some specimens of *Condylura* and *Uropsilus*, but it is very difficult to see, and I am not sure of its distribution in the other study taxa.

M. cervico-occipitalis (fig. 3)

ORIGIN: From the dorsal midline just deep to M. cervico-auriculo-frontalis.

INSERTION: Into the skin over the top of the head.

REMARKS: This muscle has the same general form in *Condylura*, *Desmana*, *Neurotrichus*, *Parascalops*, *Scalopus*, *Scapanus*, *Scaptonyx*, *Talpa*, *Uropsilus*, and *Urotrichus*.

M. cervico-auricularis, pars superficialis (fig. 3)

ORIGIN: From the dorsal midline, continuous with the posterior margin of M. cervico-occipitalis.

INSERTION: On the posteromedial edge of the auditory canal.

REMARKS: This muscle has the same general form in the 11 study taxa.

M. cervico-auricularis pars profundus (fig. 3)

ORIGIN: From the dorsal midline of the neck, deep to M. cervico-auricularis pars superficialis.

INSERTION: Into the skin over the forelimb.

REMARKS: This muscle has the same general form in *Parascalops*, *Scalopus*, *Scapanus*, and *Talpa*. In *Condylura*, *Desmana*, *Galemys*, *Neurotrichus*, *Scaptonyx*, *Uropsilus*, and *Urotrichus* it inserts with the pars superficialis on the posteromedial edge of the auditory canal.

M. occipitofrontalis

ORIGIN: From the occipital region of the skull, adjacent to the dorsal midline and just posterior and medial to M. temporalis.

INSERTION: Via a long tendon into the integument over the snout.

REMARKS: This muscle has the same general form in *Condylura*, *Desmana*, *Neurotrichus*, *Parascalops*, *Scalopus*, *Scapanus*, *Scaptonyx*, *Talpa*, *Uropsilus*, and *Urotrichus*.

M. mandibulo-auricularis

ORIGIN: From the dorsal margin of the angular process, just dorsal to M. pterygoideus internus.

INSERTION: Along the anteromedial surface of the auditory tube.

REMARKS: Similar in *Condylura*, *Desmana*, *Galemys*, *Neurotrichus*, *Parascalops*, *Scaptonyx*, *Uropsilus*, and *Urotrichus*. Present in *Talpa*, but it originates from the anterior surface of the auditory bulla directly

anterior to the meatus and from a connective tissue sheet that runs from the bulla to the posterior margin of the mandible. This muscle is greatly reduced or absent in *Scalopus* and *Scapanus*.

M. sphincter colli profundus, pars intermedia dorsalis (fig. 3)

ORIGIN: From the dorsal midline between the ear and the eye.

INSERTION: On the surface of M. platysma myoides.

REMARKS: This muscle has the same general form in *Condylura*, *Desmana*, *Neurotrichus*, *Parascalops*, *Scalopus*, *Scapanus*, *Scaptonyx*, *Talpa*, *Uropsilus*, and *Urotrichus*. The fibers of this muscle appear to cross through M. platysma myoides to form the pars intermedia ventralis. The anteriormost fibers are somewhat superficial to the remainder of the muscle and were distinguished by Meinertz (1978a) as a separate M. frontolabialis.

M. sphincter colli profundus, pars intermedia ventralis

ORIGIN: From the deep surface of M. platysma myoides.

INSERTION: In the skin of the throat region, where it decussates with its antimere.

REMARKS: This muscle has the same general form in *Condylura*, *Desmana*, *Neurotrichus*, *Parascalops*, *Scalopus*, *Scapanus*, *Scaptonyx*, *Talpa*, *Uropsilus*, and *Urotrichus*. As noted above, this muscle appears to be a continuation of the pars intermedia dorsalis that has crossed through M. platysma myoides.

Snout Muscles

The next five facial muscles have elongate, fusiform bellies and long tendons extending out into the snout, and can be considered snout muscles. Although they are found in all lipotyphlan insectivores (Dobson, 1882–1890; Butler, 1988; Whidden, 1996), the homologies relative to other mammals are unclear. I follow Dobson (1882–1890) and Gaughran (1954) in naming these muscles, but I do not mean to imply homology to the muscles of the same name in humans. The snout muscles are innervated by a branch of the facial nerve that wraps around the anteroventral side of the auditory tube. In shrews and moles they run along the zygomatic arch and insert into the snout via long tendons. Meinertz (1978a & 1978b) considered these five muscles to be parts of an M. dilator nasi.

M. zygomaticus major (figs. 5 and 7)

ORIGIN: From a small ridge just posterior to the base of the zygomatic arch.

INSERTION: Via a long tendon on the ventral surface of the nasal cartilage. This tendon runs along the upper lip just above the toothrow, around the tip of the skull, and up the ventral midline of the snout tip to the insertion.

REMARKS: This muscle has the same general form in *Condylura*, *Desmana*, *Neurotrichus*, *Parascalops*, *Scalopus*, *Scapanus*, *Scaptonyx*, *Talpa*, *Uropsilus*, and *Urotrichus*. In *Desmana*, this muscle originates from a prominent fossa at the base of the zygomatic arch.

M. zygomaticus minor (fig. 5)

ORIGIN: As an aponeurosis from a small ridge just posterior to the base of the zygomatic arch, deep to the origin of M. zygomaticus major.

INSERTION: Via a long, slender tendon that runs anteriorly along the lateral surface of the snout to insert into the lateral margin of the external naris.

REMARKS: Similar in *Desmana*, *Neurotrichus*, *Parascalops*, *Scaptonyx*, *Uropsilus*, and *Urotrichus*. In *Condylura*, the tendon for this muscle splits and extends out into the lateral nasal rays. *Scalopus* and *Scapanus* have dorsally oriented nostrils, and the insertion of this muscle is on the posterior margin of the external naris. *Talpa* has nostrils in a ventrally oriented nose pad, and the insertion of this muscle is on the ventral margin of the external naris.

M. levator alae nasi inferioris (fig. 5)

ORIGIN: As an aponeurosis from a small ridge just posterior to the base of the zygomatic arch, and also from the surface of M. levator labii superioris proprius.

INSERTION: Via a long, slender tendon on the posterior margin of the external naris.

REMARKS: This muscle has the same gen-

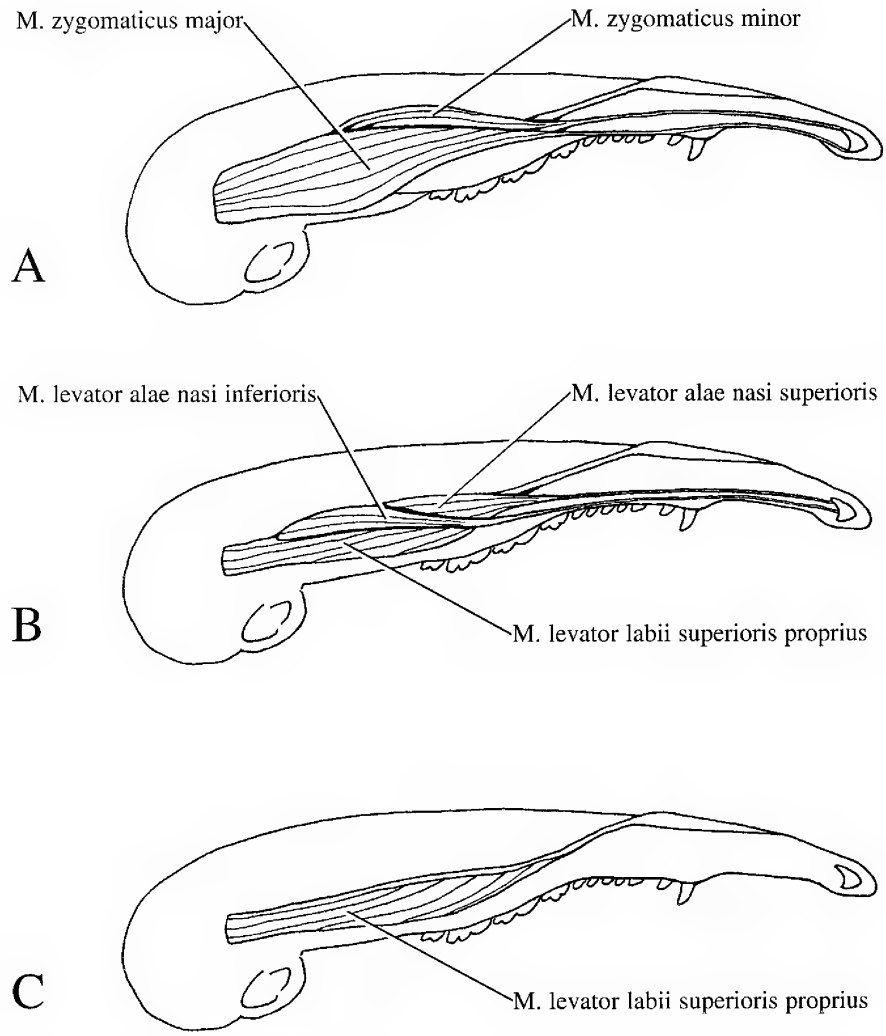

Fig. 5. Lateral view of snout muscles of *Parascalops*. **A**, Superficial layer; **B**, middle layer; **C**, deep layer.

eral form in *Condylura*, *Desmana*, *Neurotrichus*, *Parascalops*, *Scalopus*, *Scapanus*, *Scaptonyx*, *Talpa*, *Uropsilus*, and *Urotrichus*.

M. levator alae nasi superioris (fig. 5)

ORIGIN: As an aponeurosis from a small ridge just posterior to the base of the zygomatic arch and deep to M. levator alae nasi inferioris.

INSERTION: Via a long tendon on the dorsal rim of the external naris.

REMARKS: This muscle has the same general form in *Condylura*, *Desmana*, *Neurotrichus*, *Parascalops*, *Scalopus*, *Scapanus*, *Scaptonyx*, *Talpa*, *Uropsilus*, and *Urotrichus*. Gaughran (1954) incorrectly stated that M. levator alae nasi superioris is superficial to M. levator alae nasi inferioris.

M. levator labii superioris proprius (fig. 5)

ORIGIN: As a superficial head from a fossa just deep and anterior to the origin of M. zygomaticus major, and a deep head from the dorsal margin of the posterior zygomatic arch.

INSERTION: The two heads join to form a stout tendon that extends over the tip of the

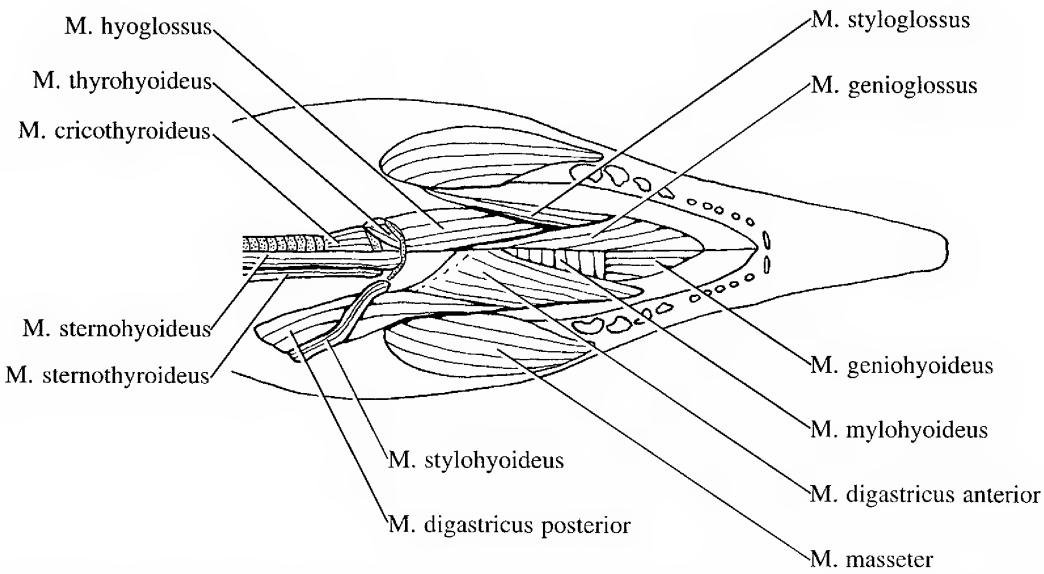

Fig. 6. Ventral view of neck muscles of *Parascalops*; superficial muscles on bottom, deeper muscles on top.

premaxilla and joins its antimere to form a flat fascial sheet that covers the cartilaginous snout tip.

REMARKS: This muscle has the same general form in the 11 study taxa. In *Condylura*, the origin of the superficial head is well anterior to the origin of the other snout muscles. This large, well-developed muscle is the deepest of the snout muscles.

M. buccinatorius

ORIGIN: From the upper jaw, just dorsal to the toothrow.

INSERTION: Along the mandible, just ventral to the toothrow.

REMARKS: This muscle has the same general form in the 11 study taxa. This muscle forms an extensive and complex mass in the cheek. The superficial fibers are transverse, and the deeper fibers are anteroventral. Fibers from M. buccinatorius extend anteriorly along both upper and lower jaws, forming M. orbicularis oris. The anterior part of M. sphincter colli profundus pars intermedia dorsalis inserts along the dorsal surface of M. buccinatorius.

M. nasolabialis superficialis (fig. 3)

ORIGIN: From the rostrum dorsal and anterior to the eye.

INSERTION: By two slightly separated slips, both into the upper lip.

REMARKS: This muscle was difficult to identify, but I found it in some specimens of *Condylura*, *Neurotrichus*, *Parascalops*, *Scalopus*, *Scapanus*, *Talpa*, *Uropsilus*, and *Urotrichus*. It may also be present in the other study taxa.

M. nasolabialis profundus (fig. 3)

ORIGIN: From the bony rostrum deep to M. nasolabialis superficialis.

INSERTION: Into the upper lip, deep to the fibers of M. orbicularis oris.

REMARKS: This muscle was difficult to identify, but I found it in some specimens of *Condylura*, *Desmana*, *Neurotrichus*, *Parascalops*, *Scalopus*, *Scapanus*, and *Talpa*. It may also be present in the other study taxa.

Hyoid Constrictor Group

M. digastricus, venter posterior (fig. 6)

The anterior portion of the digastric is discussed with the muscles of the Trigeminal Field.

ORIGIN: From the ventral base of the skull between the occipital condyle and the stylomastoid foramen, from the surface of the un-

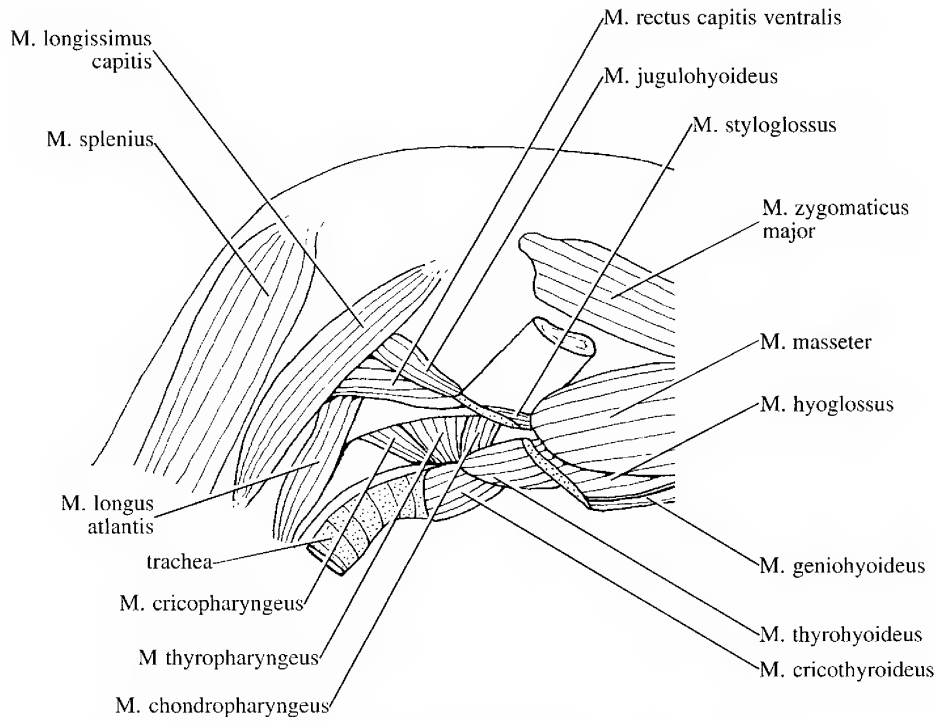

Fig. 7. Lateral view of neck muscles of *Parascalops*.

derlying M. jugulohyoideus, and from the stylohyal cartilage.

INSERTION: In a tendinous inscription into the anterior belly of the digastric.

REMARKS: This muscle has the same general form in *Condylura*, *Desmana*, *Neurotrichus*, *Parascalops*, *Scaptonyx*, *Uropsilus*, and *Urotrichus*. The stylohyal portion is especially large in *Condylura*. *Scalopus*, *Scapanus*, and *Talpa* lack fibers from the stylohyal cartilage.

M. stylohyoideus (fig. 6)

ORIGIN: From the ventrolateral surface of M. digastricus venter posterior, with some fascial attachment to the skull.

INSERTION: On the basihyal cartilage.

REMARKS: This muscle has the same general form in *Condylura*, *Neurotrichus*, *Parascalops*, *Scapanus*, *Scaptonyx*, *Talpa*, and *Urotrichus*. In *Scalopus* and *Uropsilus*, M. stylohyoideus originates medial to M. digastricus, and so does not cross over it. In *Desmana* and *Galemys*, M. stylohyoideus is either absent or indistinguishably fused with M. digastricus.

M. jugulohyoideus (fig. 7)

ORIGIN: From the posteromedial border of the stylomastoid foramen, deep to M. digastricus venter posterior.

INSERTION: On the tip of the stylohyal cartilage, near the attachment of the stylohyal to the skull.

REMARKS: This muscle has the same general form in the 11 study taxa. In *Condylura*, the stylohyal cartilage does not attach to the skull, and M. jugulohyoideus inserts on the tip of the floating cartilage.

M. stapedius

ORIGIN: From the posterior wall of a small channel that is lateral to the stylomastoid foramen on the base of the skull.

INSERTION: On the stapedial process of the stapes.

REMARKS: This muscle has the same general form in *Condylura*, *Neurotrichus*, *Parascalops*, *Scalopus*, *Scapanus*, and *Talpa*. The tendon of this tiny, triangular muscle passes through a foramen in the skull.

GLOSSOPHARYNGEAL FIELD

Glossopharyngeal Group

M. stylopharyngeus

ORIGIN: From the posterior end of the stylohyal cartilage.

INSERTION: The ventral and lateral fibers via a broad fascial sheet on the posterior surface of the ceratohyal cartilage, and the dorsal and medial fibers on the lateral wall and roof of the pharynx.

REMARKS: This muscle has the same general form in the 11 study taxa.

M. ceratohyoideus

ORIGIN: From the anterior surface of the thyrohyal cartilage.

INSERTION: On the posterior surfaces of the hypohyal and ceratohyal cartilages.

REMARKS: This muscle has the same general form in the 11 study taxa.

VAGUS FIELD

Pharyngeal Constrictor Group

M. pterygopharyngeus

ORIGIN: From the tip of the pterygoid hamulus.

INSERTION: Into the midline of the roof of the pharynx.

REMARKS: This muscle has the same general form in *Neurotrichus*, *Parascalops*, *Scalopus*, *Scapanus*, *Scaptonyx*, *Talpa*, *Uropsilus*, and *Urotrichus*. I did not observe this muscle in *Condylura*, *Desmana*, and *Galemys*. This is the anteriormost of the pharyngeal constrictors.

M. chondropharyngeus (fig. 7)

ORIGIN: From the dorsal margin of the thyrohyal cartilage.

INSERTION: Into the midline of the roof of the pharynx, just posterior to M. pterygopharyngeus.

REMARKS: This muscle has the same general form in the 11 study taxa.

M. thyropharyngeus (fig. 7)

ORIGIN: From the surface of the thyroid cartilage.

INSERTION: Into the midline of the roof of the pharynx, just posterior to M. chondropharyngeus.

REMARKS: This muscle has the same general form in the 11 study taxa.

M. cricopharyngeus (fig. 7)

ORIGIN: From the posterior surface of the cricoid cartilage.

INSERTION: Into the midline of the roof of the pharynx, just posterior to M. thyropharyngeus.

REMARKS: This muscle has the same general form in *Neurotrichus*, *Parascalops*, *Scalopus*, *Scapanus*, *Scaptonyx*, *Talpa*, and *Urotrichus*. It is absent in *Condylura*, *Desmana*, *Galemys*, and *Uropsilus*.

M. cricoarytenoideus dorsalis

ORIGIN: From the dorsal surface of the cricoid cartilage.

INSERTION: On the dorsal and posterior surfaces of the arytenoid cartilage.

REMARKS: This muscle has the same general form in *Condylura*, *Desmana*, *Neurotrichus*, *Parascalops*, *Scalopus*, *Scapanus*, and *Talpa*.

M. cricoarytenoideus ventralis

ORIGIN: From the anterior surface of the cricoid cartilage.

INSERTION: On the ventral surface of the arytenoid cartilage.

REMARKS: This muscle has the same general form in *Condylura*, *Desmana*, *Neurotrichus*, *Parascalops*, *Scalopus*, *Scapanus*, and *Talpa*.

M. cricothyroideus (figs. 6 and 7)

ORIGIN: From the posterior surface of the cricoid cartilage.

INSERTION: On the posterior edge of the thyroid cartilage.

REMARKS: This muscle has the same general form in *Condylura*, *Desmana*, *Neurotrichus*, *Parascalops*, *Scalopus*, *Scapanus*, and *Talpa*.

M. thyroarytenoideus

ORIGIN: From the inner surface of the thyroid cartilage, and also from the fascia between the thyroid and cricoid cartilages.

INSERTION: On the anterior surface of the arytenoid cartilage.

REMARKS: This muscle has the same general form in *Condylura*, *Desmana*, *Neurotrichus*, *Parascalops*, *Scalopus*, *Scapanus*, and *Talpa*.

M. arytenoideus

ORIGIN: From the posterior and lateral surfaces of the arytenoid cartilage.

INSERTION: In fascia over the dorsal midline of the larynx.

REMARKS: This muscle has the same general form in *Condylura*, *Desmana*, *Neurotrichus*, *Parascalops*, *Scalopus*, *Scapanus*, and *Talpa*.

ACCESSORY FIELD

Palatine Group

M. levator veli palatini

ORIGIN: From the base of skull just posterior to the eustachian tube.

INSERTION: On the floor of the nasopharynx.

REMARKS: This muscle has the same general form in *Condylura*, *Desmana*, *Neurotrichus*, *Parascalops*, *Scalopus*, *Scapanus*, *Scaptonyx*, *Talpa*, *Uropsilus*, and *Urotrichus*.

Trapezius Group

M. trapezius anticus, pars capitis

ORIGIN: From the midline of the occipital region of the skull.

INSERTION: On the metacromion process of the scapula.

REMARKS: This muscle is absent in *Condylura*, *Neurotrichus*, *Parascalops*, *Scalopus*, *Scapanus*, *Scaptonyx*, *Talpa*, and *Urotrichus*, but is present in *Desmana*, *Galemys*, and *Uropsilus*. Dobson (1882–1890) identified this muscle as M. occipito-scapularis externus in *Desmana* and *Galemys*, and he believed it to be a part of the rhomboideus complex.

M. trapezius anticus, pars cervicis

ORIGIN: From the dorsal midline of the neck, well posterior to the pars capitis and deep to the retroauricular muscles.

INSERTION: In fascia on the greater tuberosity of the humerus and on the humeroclavicular tendon.

REMARKS: This muscle is well developed in *Condylura*, *Desmana*, *Galemys*, *Neurotrichus*, *Scaptonyx*, *Uropsilus*, and *Urotrichus*, where it inserts on the metacromion process of the scapula, but in *Parascalops*, *Scalopus*, *Scapanus*, and *Talpa* it is reduced to a thin sheet of fibers that disappear in fascia. In *Desmana* and *Galemys*, the posteriormost fibers extend onto the vertebral border of the scapula, and in *Neurotrichus*, *Scaptonyx*, and *Urotrichus*, these posterior fibers form a separate slip that inserts on the vertebral border. Reed (1951) referred to these posterior fibers in *Neurotrichus* as a separate M. trapezius medius. In *Neurotrichus*, *Scaptonyx*, and *Urotrichus*, the origin of this muscle extends onto the occiput, but these anterior fibers are continuous with the rest of the muscle and not a pars capitis.

M. trapezius posticus (fig. 10)

ORIGIN: From the dorsal midline over the lumbar vertebrae.

INSERTION: On a tuberosity at the dorsal end of the scapular spine.

REMARKS: This muscle has the same general form in the 11 study taxa. In *Desmana* and *Galemys*, the origin of this muscle extends onto the iliac crest.

M. dorsocuticularis

ORIGIN: From fascia over the metapophysis of the third lumbar vertebra.

INSERTION: Into the skin over the back, medial to the forearm.

REMARKS: This muscle has the same general form in the 11 study taxa. It originates from over the third lumbar vertebra in *Parascalops*, *Scalopus*, *Scapanus*, and *Talpa*, from over the fourth through the sixth lumbar vertebrae in *Condylura*, *Neurotrichus*, *Scaptonyx*, and *Urotrichus*, from over the last lumbar vertebra and the iliac crest in *Uropsilus*, and from only the iliac crest in *Desmana* and *Galemys*.

M. sterno-cleido-mastoideus/occipitalis complex

This complex forms the cranioventral margin of the accessory field in mammals, and is frequently split into several parts (Howell, 1937). It varies considerably in talpids. In *Condylura*, *Desmana*, *Galemys*, and *Uropsilus*, it forms three muscular elements,

whereas in *Neurotrichus*, *Parascalops*, *Scalopus*, *Scapanus*, *Scaptonyx*, *Talpa*, and *Urotrichus*, it forms four elements. I treat these parts as four separate muscles according to their origins and insertions, but I am not confident that all the elements discussed under each name are homologous. Gaughran (1954) considered *Scalopus* to have superficial and deep parts to M. sternomastoideus, rather than the separate Mm. sternomastoideus and sterno-occipitalis that I recognize here. My account of this muscle complex in *Desmana* conflicts with that of Dobson (1882–1890). I was not able to dissect this muscle complex in *Galemys*.

M. cleido-occipitalis

ORIGIN: From the anteroventral surface of the medial end of the clavicle.

INSERTION: Via an aponeurosis on the lateral wall of the skull just posterior to M. temporalis, together with M. sterno-occipitalis.

REMARKS: This muscle has the same general form in *Condylura*, *Desmana*, *Neurotrichus*, *Parascalops*, *Scalopus*, *Scapanus*, *Scaptonyx*, *Talpa*, and *Urotrichus*. In *Uropsilus*, the origin is from the ala of the manubrium.

M. cleidomastoideus

ORIGIN: From the anterodorsal surface of the medial end of the clavicle, just dorsal to the origin of M. cleido-occipitalis.

INSERTION: Via an aponeurosis on a small ridge just posterior to the base of the zygomatic arch, together with M. sternomastoideus.

REMARKS: This muscle has the same general form in *Condylura*, *Desmana*, *Neurotrichus*, *Parascalops*, *Scalopus*, *Scapanus*, *Scaptonyx*, *Talpa*, and *Urotrichus*. An element in this position is absent in *Uropsilus*.

M. sternomastoideus

ORIGIN: From the anterior tip of the manubrium.

INSERTION: Via an aponeurosis on a small ridge just posterior to the base of the zygomatic arch, together with M. cleidomastoideus.

REMARKS: This muscle has the same general form in *Condylura*, *Neurotrichus*, *Parascalops*, *Scalopus*, *Scapanus*, *Scaptonyx*, *Talpa*, and *Urotrichus*. In *Uropsilus*, it originates from the dorsal surface of the manubrium. An element in this position is absent in *Desmana*. This is the M. sternomastoideus pars profundus of Gaughran (1954).

M. sterno-occipitalis

ORIGIN: From the anterior surface of the manubrium.

INSERTION: Via an aponeurosis on the lateral wall of the skull just posterior to M. temporalis, together with M. cleido-occipitalis.

REMARKS: This muscle has the same general form in *Desmana*, *Neurotrichus*, *Parascalops*, *Scalopus*, *Scapanus*, *Scaptonyx*, *Talpa*, *Uropsilus*, and *Urotrichus*. An element in this position is absent in *Condylura*. This is the M. sternomastoideus pars superficialis of Gaughran (1954).

MYOTOMIC MUSCULATURE

AXIAL MUSCULATURE

Lingual Group

M. genioglossus (fig. 6)

ORIGIN: From the medial surface of the anterior dentary.

INSERTION: Into the body of the tongue, meeting its antimere in the midline.

REMARKS: This muscle has the same general form in the 11 study taxa.

M. hyoglossus (figs. 6 and 7)

ORIGIN: From the anterior and ventral surfaces of the basihyal cartilage and the lateral surface of the thyrohyal cartilage.

INSERTION: Into the body of the tongue, between Mm. styloglossus and genioglossus.

REMARKS: This muscle has the same general form in the 11 study taxa.

M. styloglossus (figs. 6 and 7)

ORIGIN: From the lateral surface of the stylohyal cartilage.

INSERTION: Into the lateral part of the body of the tongue.

REMARKS: This muscle has the same general form in the 11 study taxa.

Medial Ventral Cervical Group

M. geniohyoideus (figs. 6 and 7)

ORIGIN: As a flat tendon from the ventral and medial surfaces of the anterior mandible.

INSERTION: On the anterior and ventral surfaces of the basihyal cartilage and the ventromedial surface of the thyrohyal cartilage.

REMARKS: This muscle has the same general form in the 11 study taxa. The antimeres of this muscle are largely fused and tightly attached to the midventral raphe of M. mylohyoideus profundus.

M. sternohyoideus (fig. 6)

ORIGIN: From the posterior end of the dorsal surface of the manubrium.

INSERTION: On the posterior surface of the basihyal cartilage.

REMARKS: This muscle has the same general form in the 11 study taxa.

M. sternothyroideus (fig. 6)

ORIGIN: From the posterior end of the dorsal surface of the manubrium, posterior and lateral to the origin of M. sternohyoideus.

INSERTION: Via a fascial sheet on the posterolateral margin of the thyroid cartilage.

REMARKS: This muscle has the same general form in the 11 study taxa.

M. thyrohyoideus (figs. 6 and 7)

ORIGIN: From the posterolateral margin of the ventral surface of the thyroid cartilage.

INSERTION: On the posterior surface of the basihyal and thyrohyal cartilages, lateral to the insertion of M. sternohyoideus.

REMARKS: This muscle has the same general form in the 11 study taxa.

M. omohyoideus

I did not find this muscle in the study taxa.

M. transversus hyoideus

I did not find this muscle in the study taxa. Gaughran (1954) described it for *Scalopus*.

Superficial Spino-occipital Group

M. splenius (fig. 7)

ORIGIN: From the nuchal ligament and the adjacent interscapular ligament.

INSERTION: Via an aponeurosis on the lateral occipital region of the skull.

REMARKS: This muscle has the same general form in *Parascalops*, *Scalopus*, *Scapanus*, and *Talpa*. In *Condylura*, *Desmana*, *Galemys*, *Neurotrichus*, *Scaptonyx*, *Uropsilus*, and *Urotrichus*, this muscle differs in that there are no fibers from the interscapular ligament (which is not present in these taxa), and there is a small ventral head from the median raphe of M. rhomboideus posticus.

Suboccipital Group

M. rectus capitis dorsalis major

ORIGIN: From the dorsal margin of the neural spine of the axis, and from a raphe that extends anterior to the neural spine.

INSERTION: Via a short aponeurosis on the lateral occipital region, deep to M. splenius.

REMARKS: This muscle has the same general form in *Condylura*, *Neurotrichus*, *Parascalops*, *Scalopus*, *Scapanus*, and *Talpa*.

M. rectus capitis dorsalis minor

ORIGIN: From the neural spine and anterior margin of the atlas, and from a raphe that extends anterior to the neural spine.

INSERTION: On the occipital region of the skull, deep to M. rectus capitis dorsalis major.

REMARKS: This muscle has the same general form in *Condylura*, *Neurotrichus*, *Parascalops*, *Scalopus*, *Scapanus*, and *Talpa*.

M. obliquus capitis anterior

ORIGIN: From a ridge on the lateral surface of the atlas, anterolateral to the atlantal foramen.

INSERTION: Via a fascial sheet on the lateral occipital region, superficial to M. rectus capitis dorsalis major.

REMARKS: This muscle has the same general form in *Condylura*, *Neurotrichus*, *Parascalops*, *Scalopus*, *Scapanus*, and *Talpa*.

M. obliquus capitis posterior

ORIGIN: From the lateral surface of the neural spine of the axis, and from a median raphe anterior to the spine.

INSERTION: On the posterodorsal surface of the wing of the atlas.

REMARKS: This muscle has the same general form in *Condylura*, *Neurotrichus*, *Parascalops*, *Scalopus*, *Scapanus*, and *Talpa*.

Cervical Prevertebral Group

M. rectus capitis ventralis (fig. 7)

ORIGIN: From a small fossa on the ventrolateral surface of the atlas.

INSERTION: On the ventral surface of the skull, medial to the tympanic region.

REMARKS: This muscle has the same general form in *Condylura*, *Neurotrichus*, *Parascalops*, *Scalopus*, *Scapanus*, and *Talpa*.

M. longus capitis (fig. 7)

ORIGIN: From the costal processes of the fifth and sixth cervical vertebrae.

INSERTION: On the base of the skull adjacent to the midline, and superficial and anterior to the insertion of M. rectus capitis ventralis.

REMARKS: This muscle has the same general form in *Condylura*, *Neurotrichus*, *Parascalops*, *Scalopus*, *Scapanus*, and *Talpa*.

M. longus colli

ORIGIN: An anterior portion from the anterior tip of the costal processes of the second through the sixth cervical vertebrae, and a posterior portion from the lateral surface of the seventh cervical vertebra, the ventrolateral surfaces of the first through the fourth thoracic vertebrae, and the adjacent surfaces of ribs two through five.

INSERTION: The anterior portion on the costal process of the sixth cervical vertebra and the ventral surfaces of the first six cervical vertebrae, and the posterior portion via a tendon on the posterior tip of the costal process of the sixth cervical vertebra.

REMARKS: This muscle has the same general form in *Condylura*, *Neurotrichus*, *Parascalops*, *Scalopus*, *Scapanus*, and *Talpa*. The fibers of the posterior portion run anterolaterally, and the fibers of the anterior portion run anteromedially.

M. longus atlantis (fig. 7)

ORIGIN: From the zygapophyses of the third through the fifth cervical vertebrae.

INSERTION: On the lateral surface of the atlas, ventral to the atlantal foramen.

REMARKS: This muscle has the same general form in *Condylura*, *Neurotrichus*, *Parascalops*, *Scalopus*, *Scapanus*, and *Talpa*.

Lumbar Prevertebral Group

M. quadratus lumborum

ORIGIN: From the posterior surface of the last rib, from the anapophyses of the last thoracic and first two lumbar vertebrae, and from the ventrolateral margins of the last thoracic and first three lumbar vertebrae.

INSERTION: On the anterior edges of the transverse processes of the second through the sixth lumbar vertebrae.

REMARKS: This muscle has the same general form in *Condylura*, *Neurotrichus*, *Parascalops*, *Scalopus*, *Scapanus*, and *Talpa*.

M. psoas minor

ORIGIN: From the ventrolateral margins of the second through the fourth lumbar vertebrae.

INSERTION: Via a long tendon on the iliopectineal process of the pelvic girdle.

REMARKS: This muscle has the same general form in *Condylura*, *Neurotrichus*, *Parascalops*, *Scalopus*, *Scapanus*, and *Talpa*. In *Scalopus* and *Scapanus*, there are only five lumbar vertebrae, and this muscle originates from the first three. In *Neurotrichus*, this muscle originates only from the second and third lumbar vertebrae. Reed (1951) reported that this muscle originates only from the second vertebra in *Neurotrichus*.

Lateral Cervical Group

M. scalenus (fig. 8)

ORIGIN: The main portion of this muscle originates as a series of slips from the second through the fourth or fifth ribs. There is also a dorsal slip from rib 3, and small dorsal and ventral slips from rib 1.

INSERTION: On the costal processes of the third through fifth cervical vertebrae.

REMARKS: This muscle has the same general form in the 11 study taxa.

Medial Thoraco-abdominal Group

M. rectus abdominis (fig. 8)

ORIGIN: From the lateral surface of the first rib, with superficial fibers from a fascial sheet in the middle of the abdomen.

INSERTION: On the spine of the pubis of the opposite side of the body.

REMARKS: This muscle has the same general form in the 11 study taxa.

M. pyramidalis

ORIGIN: From the superficial surface of M. rectus abdominis.

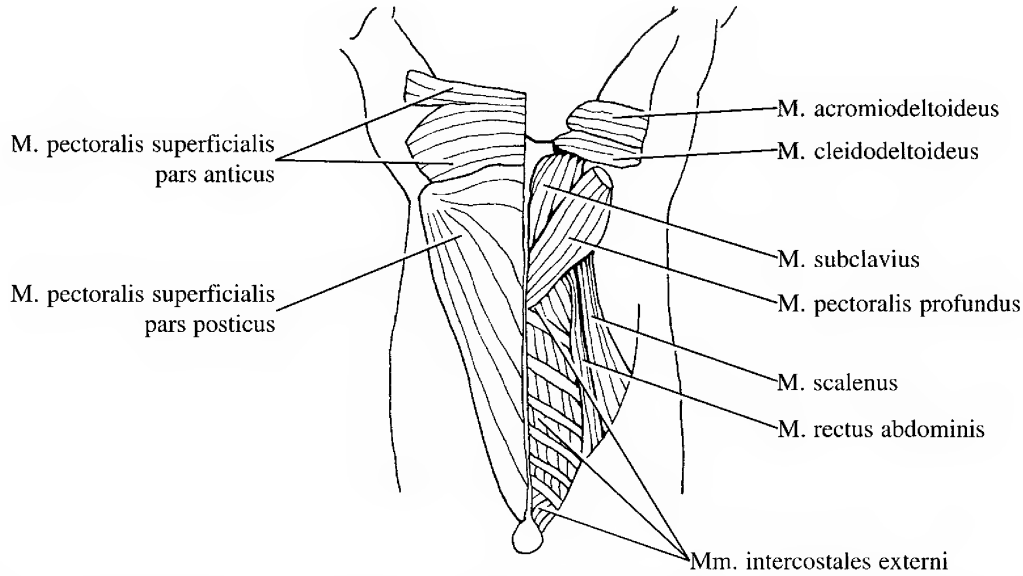

Fig. 8. Ventral view of chest muscles of *Parascalops*; superficial muscles on left, deeper muscles on right.

INSERTION: Via a short tendon on the lateral side of the spine of the pubis, lateral to the tendon of M. rectus abdominis.

REMARKS: This muscle has the same general form in the 11 study taxa. Gupta (1966) incorrectly reported that in *Scalopus* it is M. pyramidalis, not M. rectus abdominis, that crosses over the ventral midline to insert on the opposite side.

Lateral Thoraco-abdominal Group

M. serratus dorsalis anterior

ORIGIN: From the anterior surface of the interscapular ligament at the midline, dorsal to the muscular portion of M. rhomboideus posticus.

INSERTION: Via two slips, onto the dorsal surfaces of ribs 3 and 4.

REMARKS: This muscle has the same general form in *Parascalops*, *Scalopus*, *Scapanus*, and *Talpa*. *Neurotrichus*, *Scaptonyx*, and *Urotrichus* are basically similar, except that these taxa do not have an interscapular ligament, and this muscle originates from a median raphe that also gives origin to M. rhomboideus posticus. The origin in *Condylura*, *Desmana*, and *Galemys* is also from a median raphe, but insertion is via three slips, onto the dorsal surfaces of ribs 3, 4, and 5. Reed (1951) reported that this muscle inserts only on the third rib in *Neurotrichus*, but in the specimens that I dissected there were clearly slips to both the third and fourth ribs.

M. serratus dorsalis posterior

ORIGIN: From the dorsal fascia over the neural spines of the posterior thoracic and anterior lumbar vertebrae.

INSERTION: On the posterior surfaces of ribs 10–13.

REMARKS: This muscle has the same general form in the 11 study taxa.

M. sternocostalis

I did not identify this muscle in the study taxa. Dobson (1882–1890) reported its presence in *Condylura*.

Mm. intercostales externi (fig. 8)

These muscles connect adjacent ribs. They form a continuous layer from the costovertebral articulations to the costal cartilages. Adjacent to the vertebral column the fibers have an anteromedial orientation, whereas adjacent to the sternum the orientation is anterolateral. Superficial slips extend from the first rib to the third and fourth ribs, skipping over the ribs in between.

REMARKS: These muscles have the same general form in the 11 study taxa.

Mm. levatores costarum

ORIGIN: From the anterior surfaces of the ribs, just lateral to their vertebral articulations.

INSERTION: On the transverse processes of the thoracic vertebrae.

REMARKS: These muscles have the same general form in the 11 study taxa.

M. obliquus abdominis externus

ORIGIN: As a series of slips from the lateral surfaces of ribs 4–13.

INSERTION: The anteriormost fibers into fascia overlapping the lateral margin of M. rectus abdominis, the main portion of the muscle into fascia over the abdomen, and the posteriormost fibers into the inguinal region, where they form a broad fascial sheet that attaches to the horizontal ramus of the pubis.

REMARKS: This muscle has the same general form in the 11 study taxa.

M. obliquus abdominis internus

ORIGIN: From a fascial sheet over the neural spines of the lumbar and posterior thoracic vertebrae, from the crest of the ilium, from the inguinal tendon, and from the horizontal ramus of the pubis.

INSERTION: On the dorsal surfaces of the last four ribs, on the surface of M. transversus abdominis, and into the fascia covering the abdomen.

REMARKS: This muscle has the same general form in the 11 study taxa.

Mm. intercostales interni

These muscles connect adjacent ribs. They form a continuous layer from the costovertebral articulations to the costal cartilages, deep to Mm. intercostales externi. Adjacent to the vertebral column the fibers have an anterolateral orientation, whereas adjacent to the sternum the orientation is anteromedial.

REMARKS: These muscles have the same general form in *Condylura*, *Neurotrichus*, *Parascalops*, *Scalopus*, *Scapanus*, and *Talpa*.

Mm. subcostales

These muscles extend between the ribs on the medial surface of the ribcage. The fiber direction is the same as that of Mm. intercostales interni, but these muscles skip over certain ribs. They are best developed adjacent to the vertebral articulations at the dorsal midline.

REMARKS: These muscles have the same general form in *Condylura*, *Neurotrichus*, *Parascalops*, *Scalopus*, *Scapanus*, and *Talpa*.

M. transversus thoracis

ORIGIN: From the medial surface of the sternum, extending from the posterior end of the manubrium to the xiphoid process.

INSERTION: On the costal cartilages of ribs 2–7, and in a fascial sheet covering the medial surfaces of Mm. intercostales interni.

REMARKS: This muscle has the same general form in *Condylura*, *Neurotrichus*, *Parascalops*, *Scalopus*, *Scapanus*, and *Talpa*.

M. transversus abdominis

ORIGIN: From the medial surfaces of ribs 8–13, from fascia over the lumbar region, and from fascia attached to the horizontal ramus of the pubi.

INSERTION: In fascia over the abdomen, deep to M. rectus abdominis.

REMARKS: This muscle has the same general form in the 11 study taxa.

M. cremaster

Present only in males. Formed by a posterior outpocketing of the abdominal wall that encloses the testis, with fibers of Mm. obliquus abdominis internus and transversus abdominis roughly perpendicular to one another.

REMARKS: Dissected in detail only in *Parascalops*.

PECTORAL LIMB MUSCULATURE

Costo-spino-scapular Group

M. serratus ventralis cervicis

ORIGIN: As a nearly continuous sheet from the transverse processes of the third through the seventh cervical vertebrae, and from the costovertebral articulation of the first thoracic vertebra.

INSERTION: On the medial surface of the vertebral border of the scapula.

REMARKS: This muscle has the same gen-

eral form in *Parascalops* and *Talpa*. *Scalopus* and *Scapanus* are similar except the origin includes the costovertebral articulations of both the first and second thoracic vertebrae. *Condylura*, *Galemys*, *Neurotrichus*, *Scaptonyx*, *Uropsilus*, and *Urotrichus* are similar except that there is a separate posterior head that originates from the lateral surface of the first rib, rather than from its costovertebral articulation. Reed (1951) named this muscle M. serratus anterior cervicis, and Gaughran (1954) named it M. levator scapulae et serratus anterior cervicis.

M. serratus ventralis thoracis (fig. 10)

ORIGIN: From the lateral surfaces of the third through the ninth or tenth ribs.

INSERTION: On the medial surface of the vertebral border of the scapula, just posterior to the insertion of M. serratus ventralis cervicis.

REMARKS: This muscle has the same general form in *Condylura*, *Desmana*, *Galemys*, *Neurotrichus*, *Parascalops*, *Scalopus*, *Scapanus*, *Scaptonyx*, *Talpa*, and *Urotrichus*. In *Uropsilus*, it takes origin from the third through the eighth ribs. Reed (1951) named this muscle M. serratus anterior thoracis.

M. rhomboideus capitis

ORIGIN: From the occipital region of the skull, just lateral to the midline.

INSERTION: On the vertebral border of the scapula.

REMARKS: This muscle has the same general form in *Condylura*, *Desmana*, *Neurotrichus*, *Parascalops*, *Scalopus*, *Scapanus*, *Scaptonyx*, *Talpa*, *Uropsilus*, and *Urotrichus*.

M. rhomboideus cervicis

ORIGIN: From the nuchal ligament, superficial to M. splenius.

INSERTION: On the vertebral border of the scapula, just posterior to the insertion of M. rhomboideus capitis.

REMARKS: This muscle has the same general form in *Condylura*, *Desmana*, *Neurotrichus*, *Parascalops*, *Scalopus*, *Scapanus*, *Scaptonyx*, *Talpa*, *Uropsilus*, and *Urotrichus*.

M. rhomboideus posticus

In *Parascalops*, *Scalopus*, *Scapanus*, and *Talpa*, a stout, fibrous ligament that connects the vertebral borders of the scapulae has replaced much of this muscle. The antimeres of the remaining muscular portion meet in a midline raphe to form a thick, chevron-shaped muscle. The muscular portion is described below.

ORIGIN: From the neural spines of the second and third thoracic vertebrae.

INSERTION: On the anterior surface of the interscapular ligament.

REMARKS: This muscle has the same general form in *Parascalops*, *Scalopus*, *Scapanus*, and *Talpa*. In *Condylura*, *Desmana*, *Galemys*, *Neurotrichus*, *Scaptonyx*, *Uropsilus*, and *Urotrichus*, there is no interscapular ligament, and the antimeres of this muscle meet in a median raphe to form a thick, triangular mass connecting the vertebral borders of the scapulae. The connection to the vertebral neural spines is present in *Condylura*, *Desmana*, *Galemys*, and *Uropsilus*, but not in *Neurotrichus*, *Scaptonyx*, and *Urotrichus*. Reed (1951) reported that this muscle originates from the third and fourth thoracic vertebrae in *Mogera*, *Parascalops*, *Scalopus*, *Scapanus*, and *Talpa*. He also discussed some of the problems previous workers have had in determining the homologies of the forms of this muscle.

M. atlantoscapularis anterior

ORIGIN: From the ventral spine of the atlas, deep to the insertion of M. longus colli.

INSERTION: On the tip of the metacromion process of the scapula, medial to the insertion of M. trapezius anticus.

REMARKS: This muscle is present in *Condylura*, *Desmana*, *Galemys*, and *Uropsilus*, but not *Neurotrichus*, *Parascalops*, *Scalopus*, *Scapanus*, *Scaptonyx*, *Talpa*, or *Urotrichus*. Dobson (1882–1890) described this muscle (which he identified as M. levator scapulae vel claviculae) for *Desmana* (his *Myogale*), but incorrectly stated that it is absent in *Condylura*; Campbell (1939) and Reed (1951) repeated this error.

M. atlantoscapularis posterior

ORIGIN: From the ventral surface of the atlas.

INSERTION: On the vertebral border of the scapula.

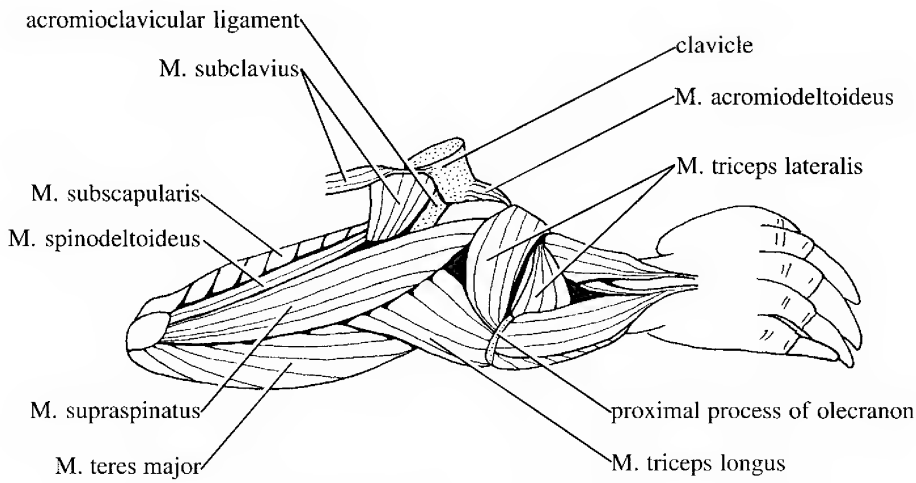

Fig. 9. Dorsal view of pectoral limb muscles of *Parascalops*.

REMARKS: Present only in *Uropsilus* among the 11 study taxa.

Latissimus-subscapular Group

M. latissimus dorsi (fig. 10)

ORIGIN: From the neural spines of the posterior thoracic vertebrae and from a fascial sheet over the entire lumbar region.

INSERTION: Via a tough aponeurosis on the surface of M. teres major.

REMARKS: This muscle has the same general form in the 11 study taxa. In *Desmana* and *Galemys*, the origin of this muscle extends onto the iliac crest. In *Uropsilus*, this muscle inserts directly on the teres tubercle of the humerus, but in the other genera it inserts on the surface of M. teres major. As noted by Campbell (1939), in *Talpa* some anteromedial fibers insert on M. teres major slightly posterior to the rest of the muscle.

M. teres major (figs. 9 and 10)

ORIGIN: From the whole of the teres fossa, from the lateral surface of the vertebral border of the scapula, and from the surface of the underlying M. subscapularis.

INSERTION: On the teres tubercle of the humerus.

REMARKS: This muscle has the same general form in *Parascalops*, *Scalopus*, *Scapanus*, and *Talpa*. In *Condylura*, *Desmana*, and *Galemys*, there is no teres fossa, and this muscle originates from the vertebral border and almost the whole lateral surface of the

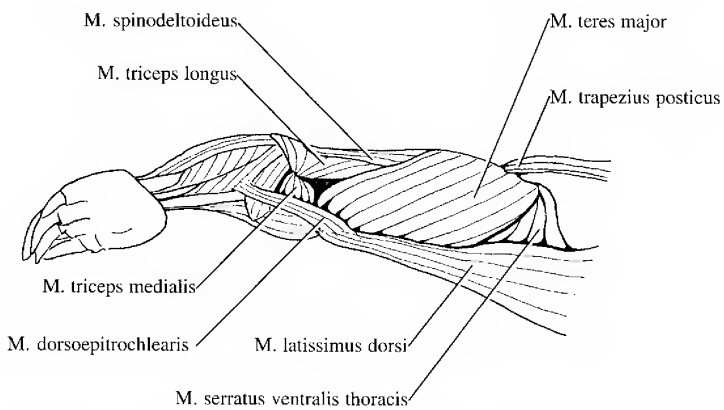

Fig. 10. Ventral view of pectoral limb muscles of *Parascalops*.

scapula. In *Neurotrichus*, *Scaptonyx*, and *Urotrichus*, the origin is largely from the surface of the underlying M. subscapularis, plus a small area at the vertebral border of the scapula. In *Uropsilus*, this muscle originates from the axillo-vertebral angle of the scapula.

M. subscapularis (fig. 9)

ORIGIN: From the subscapular fossa.

INSERTION: On the lesser tuberosity of the humerus, over the bicipital canal. Two tendinous bands extend down the length of the muscle to the insertion.

REMARKS: This muscle has the same general form in *Parascalops*, *Scalopus*, *Scapanus*, and *Talpa*. In *Desmana*, *Galemys*, and *Uropsilus*, this muscle has two heads, one originating from the subscapular fossa and the other from the axillary border of the scapula. These insert side by side on the lesser tuberosity. In *Condylura*, this muscle originates only from the subscapular fossa, and it inserts on the lesser tuberosity via two slips, each with a heavy tendinous band. In *Neurotrichus*, *Scaptonyx*, and *Urotrichus*, this muscle originates via separate heads from the subscapular fossa and the adjacent axillary border of the scapula and teres fossa; these heads fuse to form a single insertion on the lesser tuberosity.

Deltoid Group

M. cleidodeltoideus (fig. 8)

ORIGIN: From the ventral surface of the lateral end of the clavicle.

INSERTION: In the deltoid fossa, adjacent to the pectoral ridge of the humerus.

REMARKS: This muscle has the same general form in *Condylura*, *Neurotrichus*, *Parascalops*, *Scalopus*, *Scapanus*, *Scaptonyx*, *Talpa*, *Uropsilus*, and *Urotrichus*. It is similar in *Desmana* and *Galemys*, but is apparently fused with M. acromiodeltoideus.

M. acromiodeltoideus (fig. 8)

ORIGIN: From the anterodorsal margin of the lateral end of the clavicle.

INSERTION: In the deltoid fossa of the humerus, adjacent to the insertion of M. cleidodeltoideus.

REMARKS: This muscle has the same general form in *Condylura*, *Neurotrichus*, *Parascalops*, *Scalopus*, *Scapanus*, *Scaptonyx*, *Talpa*, and *Urotrichus*. In *Condylura*, *Neurotrichus*, *Scaptonyx*, and *Urotrichus*, it is well separated from M. cleidodeltoideus and inserts along the distal end of the pectoral ridge. In *Uropsilus*, it originates from the acromion process of the scapula and inserts on the pectoral ridge, distal to M. cleidodeltoideus. As mentioned above, in *Desmana* and *Galemys*, this muscle is apparently fused with M. cleidodeltoideus. Dobson (1882–1890), Freeman (1886), and Campbell (1939) failed to distinguish this muscle from M. cleidodeltoideus, possibly because of its clavicular origin in talpids other than *Uropsilus*. Reed (1951) discussed the unusual form of the deltoids in talpids.

M. spinodeltoideus (figs. 9 and 10)

ORIGIN: From a tuberosity at the vertebral end of the scapular spine, and from the length of the scapular spine.

INSERTION: On the deltoid process of the humerus.

REMARKS: This muscle has the same general form in the 11 study taxa. It is particularly well developed in *Condylura*, *Galemys*, and *Uropsilus*. Campbell (1939) and Reed (1951) discussed the problem of determining the homology of this muscle: Mm. spinodeltoideus and teres minor have similar topographic positions and innervations, and when one is missing it is impossible to be certain of the identity of the remaining muscle. I follow Reed in using the name spinodeltoideus for this muscle.

Suprascapular Group

M. supraspinatus (fig. 9)

ORIGIN: From the supraspinous fossa, from the length of the scapular spine, and from the surfaces of the adjacent Mm. subscapularis and spinodeltoideus.

INSERTION: Via a heavy, flat tendon in a small pit at the base of the greater tuberosity of the humerus.

REMARKS: This muscle has the same general form in the 11 study taxa.

M. infraspinatus

ORIGIN: From the whole of the channel-like infraspinous fossa.

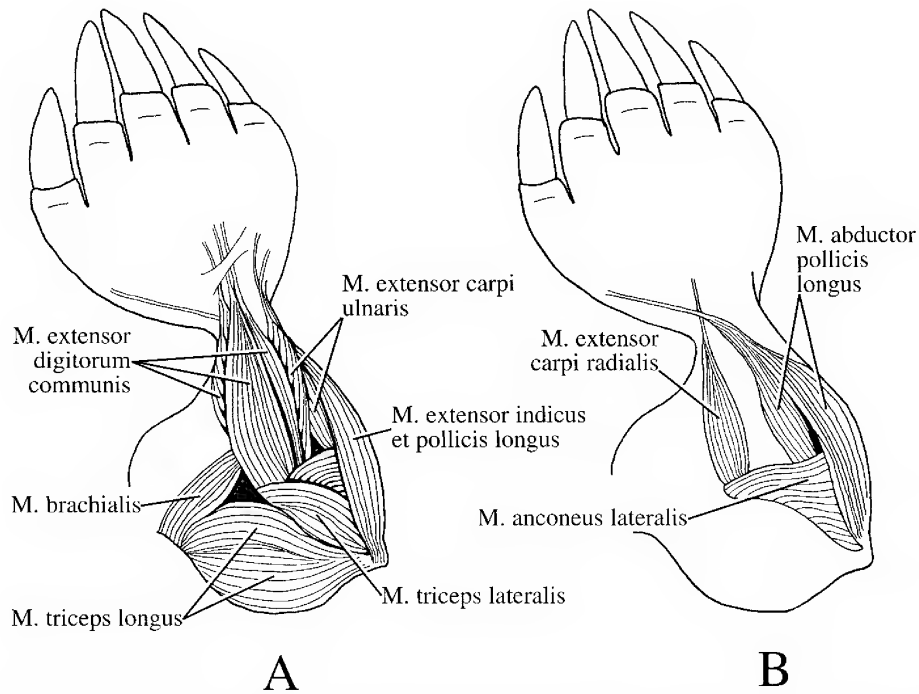

Fig. 11. Dorsal view of forearm muscles of *Parascalops*. **A**, Superficial muscles; **B**, deeper muscles.

INSERTION: Via a tendon in a small fossa between the greater tuberosity and the humeral head, lateral to the insertion of M. supraspinatus.

REMARKS: This muscle has the same general form in *Condylura*, *Desmana*, *Galemys*, *Neurotrichus*, *Parascalops*, *Scalopus*, *Scapanus*, *Scaptonyx*, *Uropsilus*, and *Urotrichus*. It is absent in *Talpa*.

Triceps Group

M. dorsoepitrochlearis (fig. 10)

ORIGIN: From the surface of M. latissimus dorsi, just posterior to the insertion of that muscle on M. teres major.

INSERTION: Into fascia over the forearm flexors.

REMARKS: This muscle has the same general form in the 11 study taxa.

M. triceps brachii, caput lateralis (figs. 9 and 11)

ORIGIN: A superficial layer from the lateral surface of the greater tuberosity of the humerus adjacent to the deltoid process, and a deep layer from the posterior surface of the humerus and the underside of the greater tuberosity.

INSERTION: Both layers on the lateral side of the posterior crest of the olecranon.

REMARKS: This muscle has the same general form in *Condylura*, *Neurotrichus*, *Parascalops*, *Scalopus*, *Scapanus*, *Talpa*, *Scaptonyx*, and *Urotrichus*. In *Desmana*, *Galemys*, and *Uropsilus*, there is only one part to this muscle, corresponding to the superficial layer in the other taxa.

M. triceps brachii, caput medialis (figs. 10 and 12)

ORIGIN: A superficial layer from the anterior surface of the humerus at the base of the teres process and from the fascial sheet covering M. teres major near its insertion, and a deep layer from the posterior surface of the humerus as far distally as the olecranon fossa.

INSERTION: The superficial layer on the palmar edge of the posterior crest of the olecranon process of the ulna, and the deep por-

tion in a fossa at the base of the proximal crest of the olecranon.

REMARKS: This muscle has the same general form in *Condylura*, *Desmana*, *Galemys*, *Neurotrichus*, *Parascalops*, *Scalopus*, *Scapanus*, *Scaptonyx*, *Talpa*, and *Urotrichus*. In *Condylura*, *Desmana*, *Galemys*, *Neurotrichus*, *Scaptonyx*, and *Urotrichus*, there are few if any fibers of the superficial layer originating from M. teres major. In *Uropsilus*, this muscle originates from the medial surface of the humerus and from the base of the teres process, and inserts on the proximal crest of the olecranon.

M. triceps brachii, caput longus (figs. 9–11)

ORIGIN: From the proximal two-thirds of the spine separating the infraspinous fossa from the teres major fossa.

INSERTION: On the proximal crest of the olecranon process of the ulna.

REMARKS: This muscle has the same general form in the 11 study taxa. It is best developed in *Parascalops*, *Scalopus*, *Scapanus*, and *Talpa*.

M. anconeus lateralis (fig. 11)

ORIGIN: From the posterior surface of the lateral epicondyle of the humerus.

INSERTION: On the lateral end of the proximal crest of the olecranon process of the ulna.

REMARKS: This muscle has the same general form in the 11 study taxa.

Forearm Extensor Group

M. brachioradialis

This muscle is absent in members of the order Insectivora (Reed, 1951).

M. supinator

ORIGIN: From the tip of the lateral epicondyle of the humerus.

INSERTION: On the medial surface of the proximal radius.

REMARKS: This muscle has the same general form in the 11 study taxa.

M. extensor carpi radialis (fig. 11)

ORIGIN: From the proximal surface of the lateral epicondyle of the humerus, and from the adjacent lateral supracondyloid ridge and posterior humeral surface.

INSERTION: Via a deep tendon that inserts on the medial surface of the third metacarpal.

REMARKS: This muscle has the same general form in the 11 study taxa. It is represented by a single element in talpids, which probably represents a fusion of longus and brevis elements (Reed, 1951).

M. abductor pollicis longus (fig. 11)

ORIGIN: A lateral head from the dorsal surface of the head of the radius, and a medial head from a fossa formed by the posterior crest of the olecranon process of the ulna.

INSERTION: Via a tendon on the medial surface of the first metacarpal, just deep to the os falciforme.

REMARKS: This muscle has the same general form in the 11 study taxa. In *Condylura*, the tendon of insertion continues past the first metacarpal to attach to the medial surface of the ungual phalanx, and in *Uropsilus*, the origin of the medial head extends well down on the shaft of the radius.

M. extensor digitorum communis (fig. 11)

ORIGIN: By superficial, medial, and deep heads, all from the lateral epicondyle of the humerus.

INSERTION: Via three long tendons, each of which splits prior to insertion. The tendons of the superficial head insert on the medial surfaces of the distal phalanges of digits IV and V, those of the medial head insert on the dorsal surfaces of the distal phalanges of digits III and IV, and those of the deep head insert on the dorsal surfaces of the distal phalanges of digits II and III.

REMARKS: This muscle has the same general form in *Condylura*, *Desmana*, *Galemys*, *Neurotrichus*, *Parascalops*, *Scalopus*, *Scapanus*, *Scaptonyx*, *Talpa*, and *Urotrichus*. In *Uropsilus*, this muscle originates as just two heads, superficial and deep. The superficial head forms a tendon that splits to insert on the medial surfaces of the distal phalanges of digits IV and V, and the deep head forms a tendon that splits to insert on the dorsal surfaces of the distal phalanges of digits II, III, and IV. There may be individual variation in the insertion of this muscle, as some of the individuals I dissected appeared to have

slightly different patterns of tendon insertion. For example, in some specimens of *Condylura*, the tendon of the superficial head sent a branch to digit II, as well as to digits IV and V. Reed (1951) described only two heads for this muscle in *Neurotrichus*, a superficial head inserting on digit V, and a deep head inserting on digits I–IV. Also, although his description of this muscle for *Scapanus* is largely similar to mine, Reed stated that the deepest head inserts only on digit II.

M. extensor indicis et pollicis longus (fig. 11)

ORIGIN: From the proximal end of the posterior crest and from the lateral side of the proximal crest of the olecranon process of the ulna.

INSERTION: Via a tendon that splits to insert on the medial sides of the distal phalanges of digits I and II.

REMARKS: This muscle has the same general form in the 11 study taxa.

M. extensor digiti quinti proprius

ORIGIN: As two heads, one by a narrow aponeurosis from the proximal crest of the olecranon process, the other from the distal surface of the lateral epicondyle of the humerus.

INSERTION: Via a single tendon on the middle phalanx of digit V.

REMARKS: This muscle has the same general form in *Parascalops*, *Scalopus*, *Scapanus*, and *Talpa*. In *Desmana*, *Galemys*, *Neurotrichus*, *Scaptonyx* and *Urotrichus*, the origin is similar, but the tendon of insertion splits, sending branches to insert on the middle phalanges of digits IV and V. In *Condylura* and *Uropsilus*, there is only one head of origin, from the lateral epicondyle, and the insertion is on the middle phalanges of digits IV and V. Reed (1951) discussed the confusing configurations in talpids of this muscle and the M. extensor carpi ulnaris.

M. extensor carpi ulnaris (fig. 11)

ORIGIN: From the lateral epicondyle of the humerus.

INSERTION: Via a tendon on the lateral surface of the second phalanx of digit IV.

REMARKS: This muscle has the same general form in *Parascalops*, *Scalopus*, *Scapanus*, and *Talpa*. In *Condylura*, *Desmana*, *Galemys*, *Neurotrichus*, *Scaptonyx*, and *Urotrichus*, this muscle originates via two heads, one from the lateral epicondyle and the other from the posterior and proximal crests of the olecranon process of the ulna. In these taxa, the insertion is also different, with the tendon attaching to a small sesamoid that overlies the ulnare. In *Uropsilus*, this muscle originates via two heads, as in the preceding taxa, but it inserts directly on the proximal end of metacarpal V. Reed (1951) offered a possible explanation for the phalangeal insertion of this muscle in *Scapanus*.

Pectoral Group

M. subclavius (figs. 8 and 9)

ORIGIN: As three poorly differentiated heads, one from the manubrium ventral to the ala, a second from the manubrium dorsal to the ala, and a third from the anterior surface of the first costal cartilage.

INSERTION: The head from the ventral manubrium broadly across the posterior surface of the clavicle, the head from the dorsal manubrium on the acromioclavicular ligament and the dorsal surface of the acromion process, and the head from the first costal cartilage via a narrow tendon on the posterior surface of the clavicle.

REMARKS: This muscle has the same general form in *Parascalops*, *Scalopus*, *Scapanus*, and *Talpa*. In *Uropsilus*, *Desmana*, and *Galemys*, it consists of a single undivided muscle mass extending from the manubrium and first rib to the clavicle. In *Uropsilus*, this muscle inserts only on the posterior surface of the clavicle, but in *Desmana* and *Galemys*, the dorsal portion inserts on the metacromion process. In *Condylura*, *Neurotrichus*, *Scaptonyx*, and *Urotrichus*, the muscle originates as three heads, as in *Parascalops*. The head from the dorsal manubrium inserts on the metacromion, the head from the ventral manubrium inserts broadly across the posterior surface of the clavicle, and the head from the first costal cartilage attaches to the posterior surface of the clavicle. This last head attaches fleshily to the clavicle in *Neurotrichus*, *Scaptonyx*, and *Urotrichus*, and via a flat tendon in *Condylura*.

The complex and variable form of this

muscle mass in talpids has led to confusion about its homology. Reed (1951) described the parts of this muscle mass as separate Mm. subclavius, costoscapularis ventralis, and costoscapularis dorsalis, and he presumed that these were three distinct muscles in the common ancestor of shrews and moles. This led him to erroneously conclude that the absence of M. costoscapularis in soricids is a secondary loss, and that previous workers on talpid myology either missed M. subclavius, failed to distinguish it from M. costoscapularis, or just forgot to describe one of the two muscles. Freeman's (1886) and Campbell's (1939) interpretations of this muscle are similar to mine.

M. pectoralis superficialis pars anticus (fig. 8)

ORIGIN: From the anterior end of the manubrium, and from a midventral raphe that extends anterior to the sternum.

INSERTION: On the medial side of the pectoral process of the humerus.

REMARKS: This muscle has the same general form in the 11 study taxa.

M. pectoralis superficialis pars posticus (fig. 8)

ORIGIN: From the lateral surface of the length of the sternum.

INSERTION: Along the lateral surface of the pectoral process of the humerus, adjacent to the lesser tuberosity.

REMARKS: This muscle has the same general form in the 11 study taxa.

M. pectoralis profundus (fig. 8)

ORIGIN: From the lateral surface of the manubrium and from the adjacent surfaces of the anterior ribs.

INSERTION: On the lateral half of the pectoral ridge of the humerus.

REMARKS: This muscle has the same general form in the 11 study taxa. In *Galemys* and *Neurotrichus*, it is difficult to separate this muscle from the overlying M. pectoralis superficialis, and it was reported as absent in these taxa by Campbell (1939) and Reed (1951), respectively.

M. pectoralis abdominalis

ORIGIN: From the fascia of Mm. rectus abdominis and obliquus externus.

INSERTION: On the pectoral crest of the humerus, adjacent to the lateralmost part of M. pectoralis superficialis pars posticus.

REMARKS: This muscle is absent in *Scalopus*, but it is present in the other study taxa.

M. cutaneus maximus

ORIGIN: As a large dorsal sheet and a smaller ventral sheet. The dorsal sheet arises from the deep surface of the dorsal integument from the base of the tail forward into the neck region, including both the dorsal and ventral surfaces of the hindlimb, and the ventral sheet arises from the deep surface of the integument of the chest region.

INSERTION: The dorsal sheet on the lateral half of the pectoral process, adjacent to M. pectoralis abdominis, and the ventral sheet on the pectoral crest, lateral to M. pectoralis superficialis posticus.

REMARKS: This muscle has the same general form in the 11 study taxa, although it is particularly well developed in *Parascalops*, *Scalopus*, *Scapanus*, and *Talpa*. Campbell (1939) incorrectly reported that the ventral portion is absent in *Neurotrichus* and *Urotrichus*; presumably he was also wrong in reporting it absent in *Mogera*, as it is well developed in *Talpa*. Where Mm. platysma and cutaneus maximus are in contact, M. cutaneus maximus is deep.

M. sternocuticularis

ORIGIN: From the ventral surface of the manubrium, between the two parts of M. pectoralis superficialis.

INSERTION: Into the integument covering the chest and the ventral surface of the forelimb.

REMARKS: This muscle is absent in *Uropsilus*, but it is present in the other study taxa. It is a narrow, straplike dermal muscle that is innervated by a branch of the pectoral nerve. It is superficial to the other muscles of the pectoral group.

Flexor Group of Arm

M. coracobrachialis

ORIGIN: From the tip of the coracoid process of the scapula.

INSERTION: On the shaft of the humerus at the proximal base of the teres tubercle.

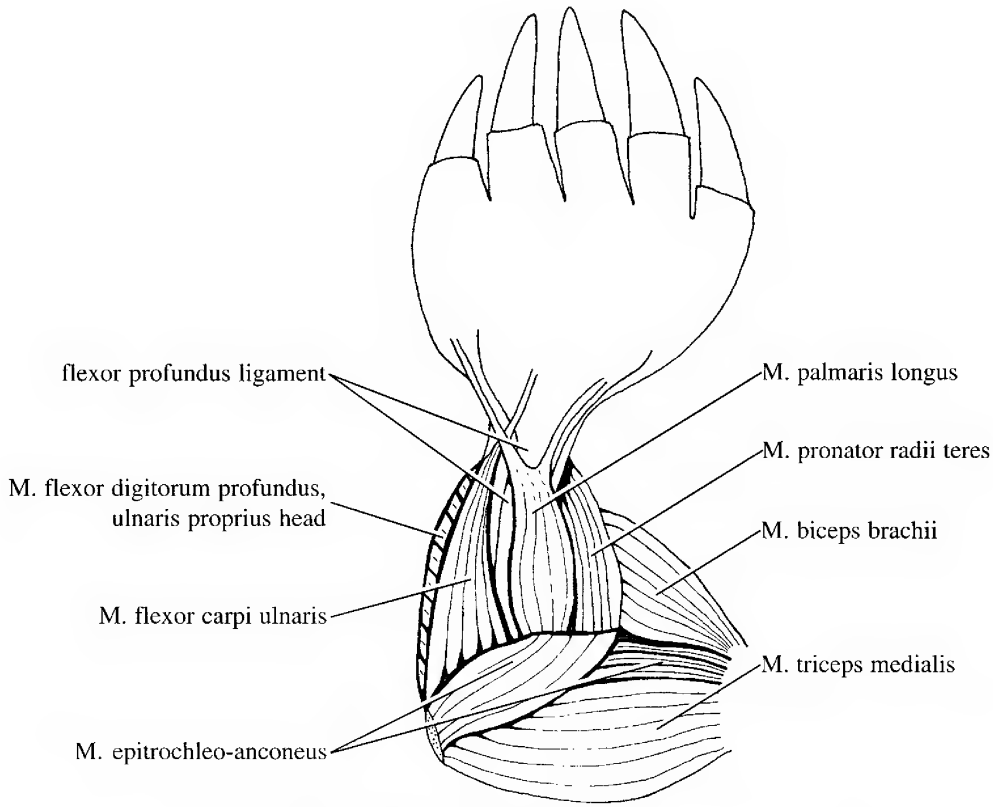

Fig. 12. Ventral view of forearm muscles of *Parascalops*.

REMARKS: I found this muscle only in *Uropsilus*.

M. biceps brachii (fig. 12)

ORIGIN: As a long tendon from the coracoid border of the rim of the glenoid fossa of the scapula. This tendon passes through a bicipital tunnel as it crosses the proximal end of the humerus.

INSERTION: On the ulnar surface of the middle of the radius.

REMARKS: This muscle has the same general form in *Parascalops* and *Talpa*, and is similar in *Scalopus* and *Scapanus* except that the insertion is via two slips, which are separated by M. pronator radii teres. *Condylura*, *Desmana*, *Galemys*, *Neurotrichus*, *Scaptonyx*, and *Urotrichus* are essentially similar, except that the insertion is at the proximal end of the radius. In *Uropsilus*, this muscle has two heads of origin, one from the tip of the coracoid process and the other via a long tendon from the rim of the glenoid fossa; insertion is on the ulnar surface of the proximal radius. Also, in *Uropsilus*, the long tendon of origin travels through a bicipital groove as it crosses the proximal end of the humerus, instead of through a tunnel as in the other study taxa.

M. brachialis (fig. 11)

ORIGIN: From an extensive area on the posterior surface of the humerus, and also from the lateral surface of the humerus distal to the greater tuberosity.

INSERTION: On the palmar surface of the ulna, just distal to the semilunar notch.

REMARKS: This muscle has the same general form in the 11 study taxa.

Flexor Group of Forearm

M. epitrochleo-anconeus (fig. 12)

ORIGIN: A large superficial head from the posterior surface of the medial epicondyle,

and a small deeper head from the posterior surface of the humerus between the trochlea and the pit for the massive ligament associated with M. flexor digitorum profundus.

INSERTION: The two heads converge on the palmar side of the proximal crest of the olecranon process of the ulna.

REMARKS: This muscle has the same general form in *Parascalops*, *Scalopus*, *Scapanus*, and *Talpa*. In *Condylura*, *Desmana*, *Galemys*, *Neurotrichus*, *Scaptonyx*, *Uropsilus*, and *Urotrichus*, the deeper fibers of this muscle do not form a second head, and instead there is a continuous origin from the posterior surface of the medial epicondyle and from the adjacent posterior surface of the humerus.

M. flexor carpi ulnaris (fig. 12)

ORIGIN: From the palmar surface of the posterior crest and the adjacent distal surface of the proximal crest of the olecranon process of the ulna.

INSERTION: Via a long tendon on the pisiform bone.

REMARKS: This muscle has the same general form in *Parascalops*, *Scalopus*, *Scapanus*, and *Talpa*. *Condylura*, *Desmana*, *Galemys*, *Neurotrichus*, *Scaptonyx*, *Uropsilus*, and *Urotrichus* have a second head of origin from the medial epicondyle of the humerus.

M. palmaris longus (fig. 12)

ORIGIN: From the palmar surface of the medial epicondyle of the humerus.

INSERTION: Via a flat tendon that forks halfway down the forearm, sending one branch to the palmar surface of the os falciforme and the other to the lateral surfaces of the phalanges of digit V.

REMARKS: This muscle has the same general form in *Condylura*, *Desmana*, *Galemys*, *Neurotrichus*, *Parascalops*, *Scalopus*, *Scapanus*, *Scaptonyx*, *Talpa*, and *Urotrichus*. In *Uropsilus*, the tendon of this muscle does not fork, but instead extends as a single tendon into the palmar fascia.

M. flexor carpi radialis

ORIGIN: From the base of the pit for the massive ligament of M. flexor digitorum profundus at the distal end of the humerus, adjacent to the entepicondylar foramen.

INSERTION: Via a tendon that passes through a groove on the lateral side of the centrale and fans out to attach to the posteroventral margins of metacarpals II and III.

REMARKS: This muscle has the same general form in *Parascalops*, *Scalopus*, *Scapanus*, and *Talpa*. In *Condylura*, *Desmana*, *Galemys*, *Neurotrichus*, *Scaptonyx*, *Uropsilus*, and *Urotrichus*, this muscle inserts only on metacarpal III. Dobson (1882–1890) described this muscle as inserting on metacarpal II in *Desmana*, but in the specimen that I dissected it inserted on metacarpal III. Reed (1951) stated that M. flexor carpi radialis inserts on metacarpal II in *Neurotrichus*, but in the three specimens of this genus that I dissected it invariably inserted on metacarpal III.

M. pronator radii teres (fig. 12)

ORIGIN: From the anterior surface of the medial epicondyle of the humerus.

INSERTION: On the pollical surface of the radius.

REMARKS: This muscle is similar in the 11 study taxa.

M. flexor digitorum superficialis

ORIGIN: As a single head from the medial epicondyle of the humerus and from the adjacent surface of a massive ligament associated with M. flexor digitorum profundus.

INSERTION: Via a tendon that broadens in the palm superficial to the flexor profundus ligament, and then sends out branches to the proximal phalanges of digits II, III, and IV. These branches are perforated by the corresponding branches of the M. flexor digitorum profundus ligament.

REMARKS: This muscle has the same general form in *Parascalops*, *Scalopus*, *Scapanus*, and *Talpa*. In *Condylura*, *Desmana*, *Galemys*, *Neurotrichus*, *Scaptonyx*, *Uropsilus*, and *Urotrichus*, this muscle originates as three distinct heads, and these form separate tendons that insert on the proximal phalanges of digits II, III, and IV. These tendons are also perforated by the corresponding branches of the M. flexor digitorum profundus ligament. In *Uropsilus*, the three heads originate from the medial epicondyle of the humerus, and in *Desmana* and *Galemys*, they originate from the area between the trochlea

and the pit for the massive ligament associated with M. flexor digitorum profundus. In *Condylura*, *Neurotrichus*, *Scaptonyx*, and *Urotrichus*, the superficial head originates from the surface of the flexor profundus ligament, and the other two heads originate from the area between the trochlea and the pit for the ligament of M. flexor digitorum profundus. The three heads of this muscle are sometimes referred to as the condylo-ulnaris, centralis, and condylo-radialis (Howell, 1936; Reed, 1951). Reed (1951) named this muscle M. flexor digitorum sublimus. His treatment of it is similar to mine, except that he described the superficial head in *Neurotrichus* as originating from the medial epicondyle of the humerus.

M. flexor digitorum profundus

In *Uropsilus*, this muscle has five muscular heads, but in the other study taxa, a massive ligament has apparently replaced one of the heads. This flexor ligament originates from a prominent pit on the distal tip of the medial epicondyle of the humerus and receives contributions from the remaining muscular heads before splitting to insert on each of the five digits. Reed (1951) reported that *Neurotrichus* has five muscular heads to this muscle, but I found only four in the specimens of *Neurotrichus* that I dissected, and I believe that he was in error. I use Reed's (1951) names for these muscles, but I come to different conclusions about the homologies of two of these muscles in *Neurotrichus* relative to the other taxa. Thompson (1884) was the first to describe the function of the flexor ligament.

ulnaris proprius head (fig. 12)

ORIGIN: From the palmar surface of the proximal half of the ulna.

INSERTION: Via a tendon that runs superficial to the great flexor ligament and joins the superficial surface of the ligament at the level of the carpus.

REMARKS: This muscle has the same general form in the 11 study taxa.

condylo-ulnaris head

ORIGIN: From the palmar surface of the ulna, distal to the semilunar notch and deep to the ulnaris proprius head.

INSERTION: On the surface of the flexor tendon adjacent to the insertion of the radialis proprius head.

REMARKS: This muscle has the same general form in *Neurotrichus*, *Parascalops*, *Scalopus*, *Scapanus*, *Scaptonyx*, *Talpa*, and *Urotrichus*. In *Condylura*, *Desmana*, and *Galemys*, this muscle has a similar origin, but it is closely associated with the ulnaris proprius, and together they form a common tendon that inserts on the superficial surface of the flexor ligament. The origin is similar in *Uropsilus*, but the tendon remains single until it joins in a common palmar tendon. Reed (1951) identified this head as the condylo-radialis in *Neurotrichus*. Castiella et al. (1992) did not describe this head for *Talpa*.

centralis head

ORIGIN: From the distal humerus between the trochlea and the pit for the flexor ligament.

INSERTION: Via a tendon that runs deep to the flexor ligament and joins the ligament along its lateral surface just proximal to the carpus.

REMARKS: This muscle has the same general form in *Condylura*, *Desmana*, *Galemys*, *Parascalops*, *Scalopus*, *Scapanus*, *Talpa*, and *Uropsilus*. In *Neurotrichus*, *Scaptonyx*, and *Urotrichus*, it originates from the palmar surface of the proximal olecranon, deep to the ulnaris proprius head; insertion is similar to the other taxa. Reed (1951) identified this muscle as the condylo-ulnaris in *Neurotrichus*.

condylo-radialis head

ORIGIN: From the anterior surface of the medial epicondyle of the humerus.

INSERTION: Forms a heavy tendon that is joined by the other heads of this muscle before splitting to send branches to the distal phalanges of the five digits.

REMARKS: This head is muscular only in *Uropsilus*, but for several reasons I believe it is homologous with the flexor ligament of the other study taxa. In *Uropsilus*, this head and the radialis proprius head form a large common tendon that is joined by contributions from the other muscular heads, similar to the way these tendons join the flexor ligament in the other study taxa. Also, in *Urop-*

silus, this head originates from the anterior surface of the medial epicondyle, which is where the flexor ligament originates. Finally, this muscular head and the flexor tendon are never found in conjunction.

radialis proprius head

ORIGIN: From the ulnar surface of the proximal radius.

INSERTION: Joins with the condylo-radialis head to insert directly on the deep surface of the middle of the flexor ligament.

REMARKS: This muscle has the same general form in *Condylura*, *Desmana*, *Galemys*, *Neurotrichus*, *Parascalops*, *Scaptonyx*, and *Urotrichus*. In *Uropsilus*, this muscle originates from the palmar surface of the middle radius and joins with the condylo-radialis head to form a stout tendon, which is joined at the level of the carpus by separate tendons from the other three heads. This head is apparently absent in *Scalopus*, *Scapanus*, and *Talpa*.

M. pronator quadratus

I did not identify this muscle in the study taxa. Reed (1951) used a compound microscope to identify muscle fibers in *Neurotrichus* that he attributed to M. pronator quadratus.

Superficial Podial Series

M. abductor pollicis brevis

ORIGIN: From a ridge on the medial side of the palmar surface of the radiale.

INSERTION: On the medial side of a sesamoid that lies on the palmar surface of the metacarpo-phalangeal joint of digit I.

REMARKS: This muscle has the same general form in *Condylura*, *Desmana*, *Neurotrichus*, *Parascalops*, *Scapanus*, *Scaptonyx*, *Talpa*, *Uropsilus*, and *Urotrichus*. It is apparently absent in *Galemys* and *Scalopus*. Reed (1951) found this muscle in *Scapanus*, but considered it to be the medial deep podial flexor for the pollex. However, in *Uropsilus* and in the soricids *Crocidura* (Haines, 1955), *Suncus* (Sharma, 1958), and *Blarina* (personal obs.), a muscle originating from a ridge on the radiale is present in addition to a full set of paired Mm. flexores breves to each digit. Such a muscle is also present in *Desmana*, which has an unpaired M. flexor brevis for each digit (see description of Mm. flexores breves below). It seems to me more likely that talpids other than *Galemys* and *Scalopus* have retained M. abductor pollicis brevis and (except for *Uropsilus*) reduced or lost the set of deep podial flexors.

M. abductor digiti quinti

ORIGIN: From the distal surface of the pisiform.

INSERTION: On the lateral side of a sesamoid that lies on the palmar surface of the metacarpo-phalangeal joint of digit V.

REMARKS: I found this tiny muscle in *Uropsilus* and *Desmana* and in some specimens of *Condylura*, *Parascalops*, and *Scapanus*. In *Uropsilus*, the palmar sesamoids between the metacarpals and the proximal phalanges are paired, and this muscle inserts on the lateral sesamoid associated with digit V. The variable occurrence of this muscle in *Condylura*, *Parascalops*, and *Scapanus* may reflect individual variation, or it may be the result of poor specimen preservation or observational error.

M. flexor brevis digitorum manus

I did not identify this muscle in any of the study taxa, although I did find it in *Blarina*.

Deep Podial Series

Mm. flexores breves (fig. 13)

In *Uropsilus*, there is a medial and a lateral flexor for each digit. These muscles originate from connective tissue over the carpo-metacarpal joints, and insert on either side of the paired sesamoids that lie on the palmar surfaces of the metacarpo-phalangeal joints. *Galemys* is similar, except that the tendons insert in connective tissue on the sides of the digits. *Galemys* also has a heavy ligament between each pair of muscles. This ligament originates from the metacarpal and attaches to the metacarpo-phalangeal sesamoid (the metacarpo-phalangeal sesamoids are single in talpids other than *Uropsilus*). In *Desmana*, there is a single flexor brevis element for each digit, and this originates from connective tissue over the carpo-metacarpal joint and inserts on the appropriate metacarpo-phalangeal sesamoid. In the other study taxa,

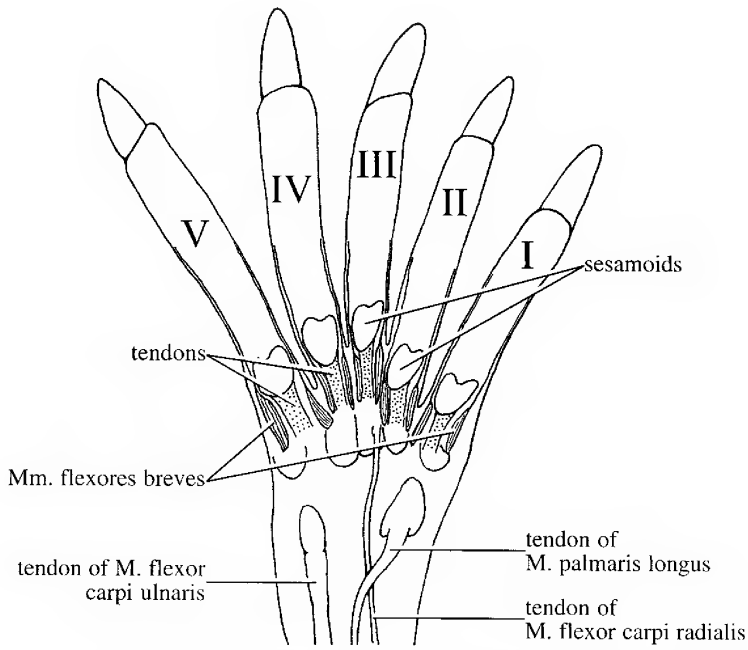

Fig. 13. Intrinsic muscles of the manus of *Galemys*.

the Mm. flexores breves have apparently been lost or replaced by tendons.

REMARKS: Reed (1951) discussed the use of the name "flexores breves" for the deep podial flexors in soricids and talpids. In the Remarks section for M. abductor pollicis brevis, I noted how my interpretation of Mm. flexores breves differs from his.

PELVIC LIMB MUSCULATURE

Iliacus Group

M. iliacus (fig. 15)

ORIGIN: From the ventral surface of the ramus of the ilium and from the ventral surfaces of the last lumbar and first sacral vertebrae.

INSERTION: On the lesser trochanter of the femur, distal to the insertion of M. psoas major.

REMARKS: This muscle has the same general form in *Condylura*, *Galemys*, *Neurotrichus*, *Parascalops*, *Scalopus*, *Scapanus*, *Scaptonyx*, *Talpa*, *Uropsilus*, and *Urotrichus*. Mm. iliacus and psoas major lie close together, inserting side by side on the lesser trochanter, and Leche (1883) considered them one muscle, M. iliopsoas.

M. psoas major

ORIGIN: From the ventral surfaces of the last three or four lumbar and the first sacral vertebrae, and from the tendon of M. psoas minor.

INSERTION: On the lesser trochanter of the femur.

REMARKS: This muscle has the same general form in *Condylura*, *Galemys*, *Neurotrichus*, *Parascalops*, *Scalopus*, *Scapanus*, *Scaptonyx*, *Talpa*, and *Uropsilus*.

M. pectineus (fig. 16)

ORIGIN: From the posterior end of the ramus of the ilium and from the anterior end of the horizontal ramus of the pubis.

INSERTION: On a ridge on the ventromedial surface of the proximal half of the femur, starting just distal to the lesser trochanter.

REMARKS: This muscle has the same general form in *Condylura*, *Desmana*, *Galemys*, *Neurotrichus*, *Parascalops*, *Scalopus*, *Scapanus*, *Scaptonyx*, *Talpa*, and *Uropsilus*.

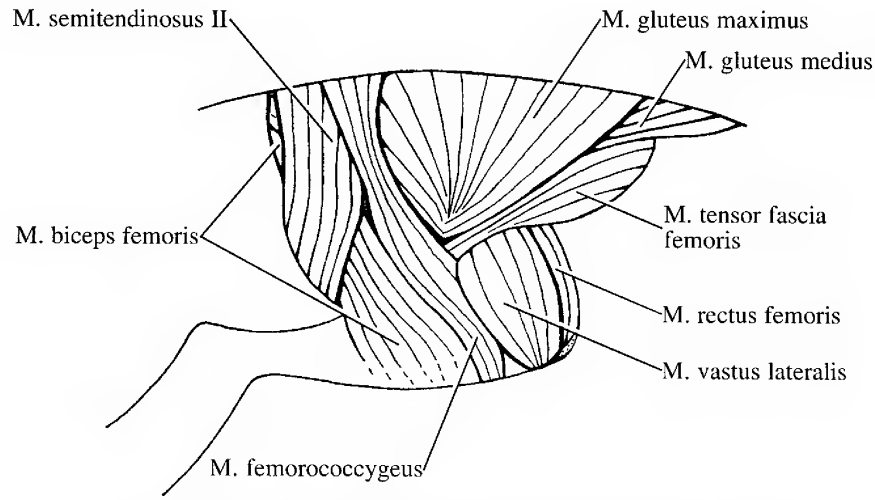

Fig. 14. Lateral view of pelvic limb muscles of *Parascalops*.

Gluteal Group

M. tensor fascia femoris (fig. 14)

ORIGIN: From the dorsal surface of the iliac crest.

INSERTION: On the third trochanter of the femur.

REMARKS: This muscle has the same general form in *Condylura*, *Desmana*, *Galemys*, *Neurotrichus*, *Parascalops*, *Scalopus*, *Scapanus*, *Talpa*, *Uropsilus*, and *Urotrichus*.

M. gluteus maximus (fig. 14)

ORIGIN: From a fascial sheet that runs between the iliac crest and the sacral neural spines, and from the anterior four or five sacral neural spines.

INSERTION: On the third trochanter of the femur, deep to the insertion of M. tensor fascia femoris.

REMARKS: This muscle has the same general form in *Condylura*, *Desmana*, *Galemys*,

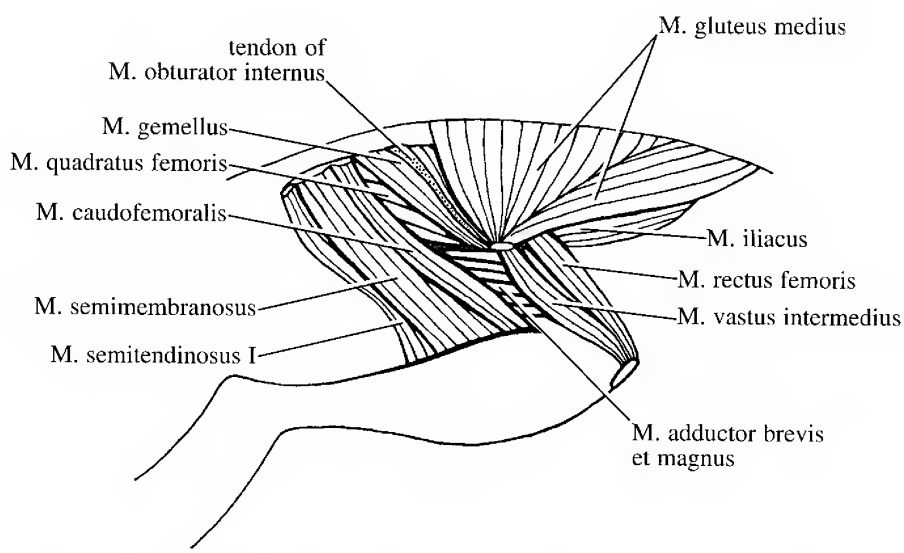

Fig. 15. Lateral view of pelvic limb muscles of *Parascalops*, superficial muscles removed.

Neurotrichus, *Parascalops*, *Scalopus*, *Scapanus*, *Talpa*, *Uropsilus*, and *Urotrichus*. Leche (1883) incorrectly reported that this muscle inserts on the greater trochanter.

M. femorococcygeus (fig. 14)

ORIGIN: From a fascial sheet attaching to the sacral spine and from the surface of M. gluteus maximus.

INSERTION: Via a fascial sheet that attaches to the falciform process and crest of the tibia, and that covers the adjacent surface of the shank.

REMARKS: This muscle has the same general form in *Condylura*, *Galemys*, *Neurotrichus*, *Parascalops*, *Scalopus*, *Scapanus*, *Talpa*, and *Urotrichus*. In *Uropsilus*, this muscle does not originate from the surface of M. gluteus maximus, but it is otherwise similar. In *Desmana*, some anterior fibers of this muscle originate from the third trochanter of the femur and join the fascial sheet of the main part of the muscle to insert on the falciform process. These fibers represent one head of Dobson's (1882–1890) M. biceps flexor cruris, with the other heads being the remainder of M. femorococcygeus plus Mm. biceps femoris and tenuissimus.

M. tenuissimus

ORIGIN: From the dorsal margin of the lateral surface of the sacral spine, deep to M. femorococcygeus.

INSERTION: On the Achilles tendon, deep to the insertion of M. biceps femoris.

REMARKS: This muscle has the same general form in *Condylura*, *Desmana*, *Galemys*, *Neurotrichus*, *Parascalops*, *Scalopus*, *Scapanus*, *Talpa*, *Uropsilus*, and *Urotrichus*.

M. gluteus medius (figs. 14 and 15)

ORIGIN: From the iliac crest, from the dorsolateral surface of the ilium, and from the sacral spine of the first four sacral vertebrae.

INSERTION: On the greater trochanter of the femur.

REMARKS: This muscle has the same general form in *Condylura*, *Desmana*, *Galemys*, *Neurotrichus*, *Parascalops*, *Scalopus*, *Scapanus*, *Talpa*, *Uropsilus*, and *Urotrichus*.

M. gluteus minimus

This muscle is either absent or fused to M. gluteus medius in soricoids (shrews and moles) (Reed, 1951).

M. piriformis

This muscle is absent in soricoids (shrews and moles) (Reed, 1951).

Quadriceps Femoris Group

M. rectus femoris (figs. 14–18)

ORIGIN: From a small process at the anterodorsal margin of the acetabulum of the pelvis.

INSERTION: On the anterior and dorsal surfaces of the patella.

REMARKS: This muscle has the same general form in the 11 study taxa. Distally, M. rectus femoris becomes partially fused with the three vasti muscles, forming a quadriceps femoris, but the four elements are still largely separable.

M. vastus lateralis (figs. 14 and 17)

ORIGIN: From the anterior surface of the proximal femur, between the greater and third trochanters.

INSERTION: On the lateral surface of the patella.

REMARKS: This muscle has the same general form in the 11 study taxa.

M. vastus medialis (figs. 16 and 18)

ORIGIN: From the anteromedial surface of the proximal half of the femur, distal to the lesser trochanter.

INSERTION: On the medial surface of the patella.

REMARKS: This muscle has the same general form in the 11 study taxa.

M. vastus intermedius (fig. 15)

ORIGIN: From the anterior surface of the middle of the femur.

INSERTION: Via a short flat tendon on the dorsal surface of the patella.

REMARKS: This muscle has the same general form in the 11 study taxa.

M. sartorius

This muscle is absent in soricoids (shrews and moles) (Reed, 1951).

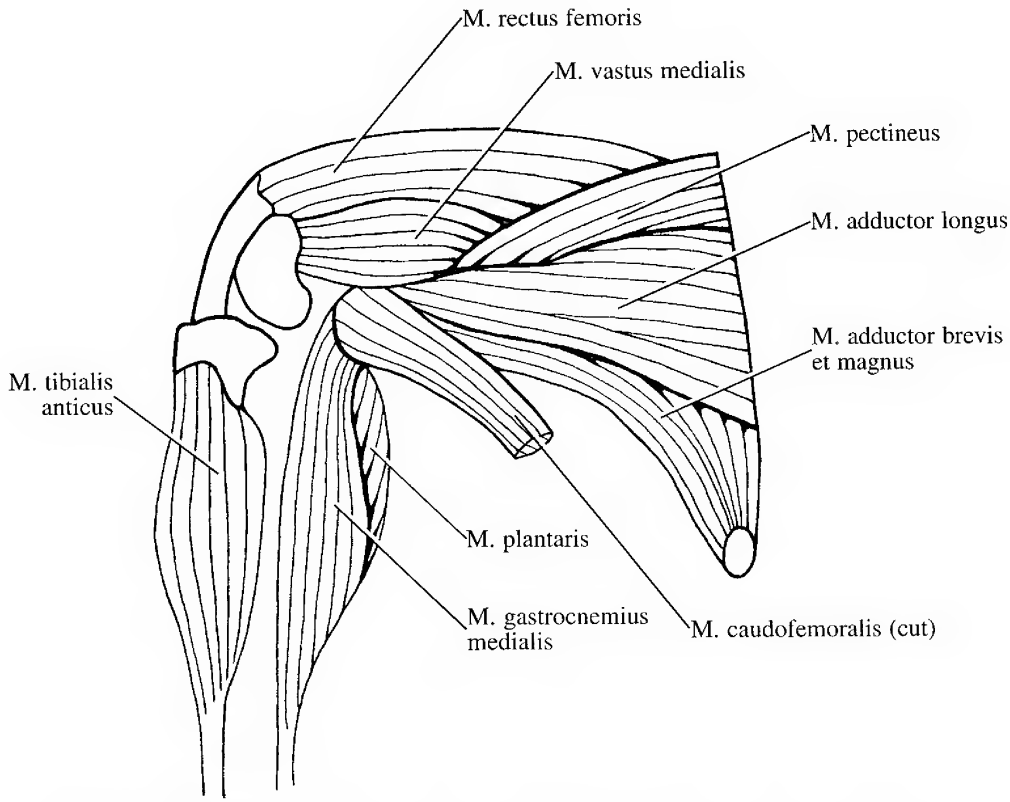

Fig. 16. Medial view of pelvic limb muscles of *Parascalops*, M. gracilis removed.

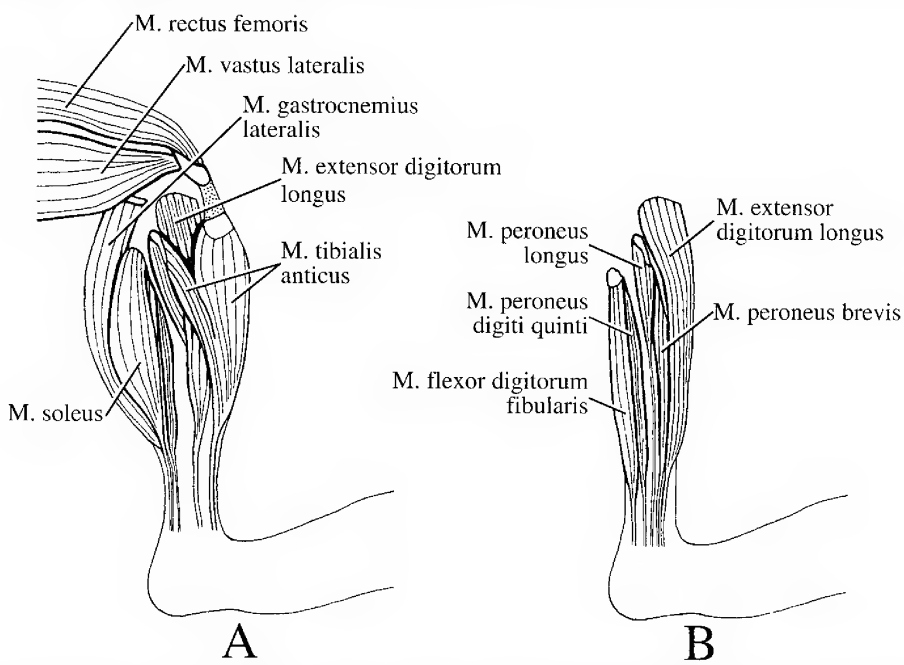

Fig. 17. Lateral view of lower leg muscles of *Parascalops*. **A**, Superficial muscles; **B**, deeper muscles.

Tibial Extensor Group

M. extensor digitorum longus (fig. 17)

ORIGIN: From the anterior surface of the lateral epicondyle of the femur.

INSERTION: Via four tendons on the dorsal surfaces of the distal phalanges of digits II–V: the most superficial tendon goes to digit II, the next to digit III, the next to digit IV, and the deepest to digit V.

REMARKS: This muscle has the same general form in *Condylura*, *Desmana*, *Galemys*, *Parascalops*, *Scalopus*, *Scapanus*, *Talpa*, and *Uropsilus*. In *Neurotrichus*, *Scaptonyx*, and *Urotrichus*, there is an additional head of origin from the anterior surface of the lateral process of the fibula.

M. extensor hallucis longus

ORIGIN: From the ventral edge of the falciform process and the adjacent lateral surface of the tibia.

INSERTION: Via a tendon on the dorsal surface of the distal phalanx of digit I.

REMARKS: This muscle has the same general form in *Condylura*, *Desmana*, *Galemys*, *Neurotrichus*, *Parascalops*, *Scalopus*, *Scapanus*, *Scaptonyx*, *Talpa*, and *Urotrichus*. *Uropsilus* is similar, except that the tendon of insertion splits and inserts on digits I and II.

M. tibialis anticus (figs. 16–18)

ORIGIN: From the lateral and distal surfaces of the falciform process of the tibia, from the lateral surface of the proximal tibial shaft, and from the anteromedial surface of the lateral process of the fibula and a fascial sheet between the lateral process and the falciform process.

INSERTION: Via a stout tendon into a pit on the medial surface of tarsale I.

REMARKS: This muscle has the same general form in *Condylura*, *Desmana*, *Galemys*, *Neurotrichus*, *Parascalops*, *Scaptonyx*, *Uropsilus*, and *Urotrichus*. In *Scalopus*, *Scapanus*, and *Talpa*, there is no head of origin from the lateral process of the fibula, and much of this muscle originates from a fossa on the anteromedial surface of the tibial head.

Peroneal Group

M. peroneus longus (fig. 17)

ORIGIN: A superficial head from the posterior surface of the lateral process of the fibula, and a deep head from the lateral condyle of the tibia.

INSERTION: Via a long tendon that runs through a channel on the distal surface of the calcaneus and then forks, with the branches attaching on the ventral surfaces of metatarsals I and III.

REMARKS: This muscle has the same general form in the 11 study taxa. Reed (1951) reported that this muscle inserts only on metatarsal I in *Scapanus*, and that in *Neurotrichus* it forks, with one branch inserting on metatarsal I and the other branch forming one of the Mm. flexores breves to digit II.

M. peroneus brevis (fig. 17)

ORIGIN: A superficial head from the distal tip of the lateral process of the fibula, and a deep head from the interosseous membrane and the lateral surface of the tibia proximal to its fusion with the fibula.

INSERTION: Via a tendon that runs behind the lateral malleolus, passes through a shallow groove in the dorsal surface of the calcaneus, and attaches to the proximal end of metatarsal V.

REMARKS: This muscle has the same general form in the 11 study taxa.

M. peroneus digiti quarti

ORIGIN: From the lateral surface of the fibula at the base of the lateral process.

INSERTION: On the proximal end of the middle phalanx of digit IV.

REMARKS: This muscle is present in *Condylura*, *Desmana*, *Galemys*, *Neurotrichus*, *Scaptonyx*, *Uropsilus*, and *Urotrichus*. It is absent in *Parascalops*, *Scalopus*, *Scapanus*, and *Talpa*.

M. peroneus digiti quinti (fig. 17)

ORIGIN: From the lateral surface of the fibula at the base of the lateral process.

INSERTION: On the proximal end of the middle phalanx of digit V.

REMARKS: This muscle has the same general form in the 11 study taxa.

Adductor Group

M. gracilis

ORIGIN: From the ventrolateral surface of the horizontal ramus of the pubis.

INSERTION: Via a fascial sheet onto the anterior surface of the falciform process of the tibia.

REMARKS: This muscle has the same general form in the 11 study taxa.

M. adductor longus (fig. 16)

ORIGIN: From the ventrolateral surface of the middle of the horizontal ramus of the pubis.

INSERTION: Largely on the posterior surface of the shaft of the femur, with a small posterior slip on the proximal surface of the medial epicondyle.

REMARKS: This muscle has the same general form in the 11 study taxa. In *Condylura*, the two parts of this muscle are approximately equal in size.

M. adductor brevis et magnus (figs. 15 and 16)

ORIGIN: From the ventrolateral surface of the posterior half of the horizontal ramus of the pubis, and down the descending ramus to the pubic spine.

INSERTION: Onto a ridge on the posterolateral side of the femur, extending from the posterior surface of the third trochanter almost to the lateral epicondyle.

REMARKS: This muscle has the same general form in the 11 study taxa. Mm. adductor brevis and adductor magnus are fused in shrews and moles (Leche, 1883).

M. obturator externus

ORIGIN: From the lateral surface of the horizontal ramus of the pubis.

INSERTION: In the intertrochanteric fossa of the femur.

REMARKS: This muscle has the same general form in the 11 study taxa.

Ischiotrochanteric Group

M. obturator internus (fig. 15)

ORIGIN: From the medial surface of the anterior half of the horizontal ramus of the pubis.

INSERTION: Via a flat tendon that runs through the sciatic notch and over the dorsal margin of the acetabulum, superficial to M. gemellus, to insert on the posteroproximal surface of the greater trochanter of the femur.

REMARKS: This muscle has the same general form in *Condylura*, *Neurotrichus*, *Parascalops*, *Scalopus*, *Scapanus*, *Scaptonyx*, *Talpa*, *Uropsilus*, and *Urotrichus*. This muscle is apparently absent in *Desmana* and *Galemys*. Dobson (1882–1890) also noted the absence of this muscle in *Desmana*.

M. gemellus (fig. 15)

ORIGIN: From the dorsolateral surface of the horizontal ramus of the ischium.

INSERTION: On the proximal margin of the posterior surface of the greater trochanter of the femur.

REMARKS: This muscle has the same general form in *Condylura*, *Desmana*, *Galemys*, *Neurotrichus*, *Parascalops*, *Uropsilus*, and *Urotrichus*. In *Scalopus*, *Scapanus*, and *Talpa*, this muscle is fused at its origin with M. quadratus femoris. Dobson (1882–1890) incorrectly reported that this muscle is absent in *Desmana*.

M. quadratus femoris (fig. 15)

ORIGIN: From the posterior end of the ischium and from the lateral surface of the descending ramus of the pubis.

INSERTION: On the posteromedial surface of the lesser trochanter of the femur.

REMARKS: This muscle has the same general form in *Condylura*, *Desmana*, *Galemys*, *Neurotrichus*, *Parascalops*, *Uropsilus*, and *Urotrichus*. In *Scalopus*, *Scapanus*, and *Talpa*, the origin of this muscle is more extensive, extending deep to M. gemellus as far anteriorly as the posterior rim of the acetabulum. Its fusion with M. gemellus in these three genera has already been noted.

Hamstring Group

M. caudofemoralis (figs. 15 and 16)

ORIGIN: From the ischial tuberosity, deep to M. biceps femoris.

INSERTION: In a small fossa on the medial epicondyle of the femur.

REMARKS: This muscle has the same general form in the 11 study taxa. Reed (1951)

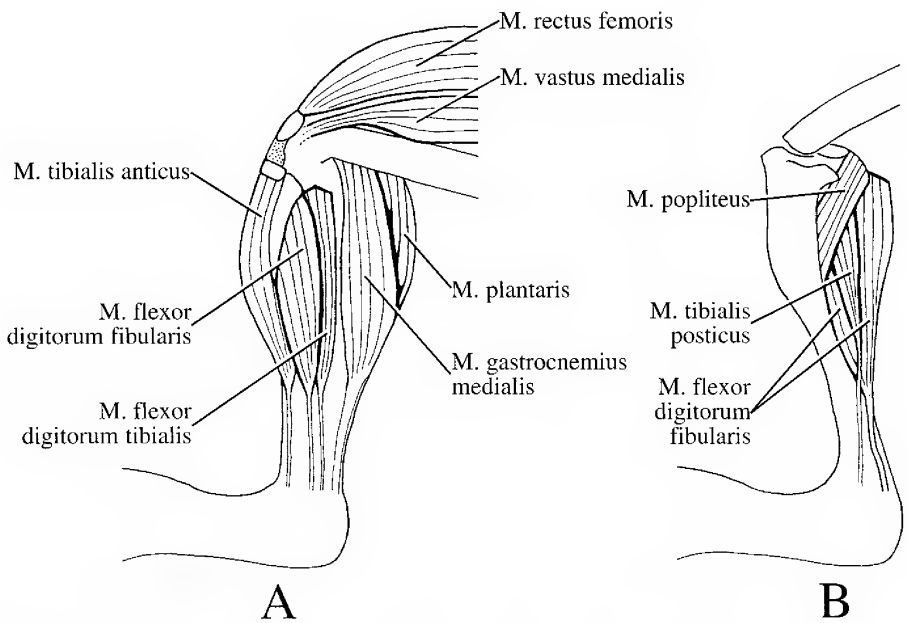

Fig. 18. Medial view of lower leg muscles of *Parascalops*. **A**, Superficial muscles; **B**, deeper muscles.

discussed past confusion over the homology of this muscle.

M. semitendinosus I (fig. 15)

ORIGIN: From the ventral surface of the descending ramus of the pubis and the tip of the pubic spine.

INSERTION: Via a fascial sheet on the anterior surface of the tibial crest.

REMARKS: This muscle has the same general form in the 11 study taxa. The two heads of the typical mammalian semitendinosus are separate muscles in shrews and moles and were designated Mm. semitendinosus I and II by Leche (1883).

M. semitendinosus II (fig. 14)

ORIGIN: From the posterior end of the sacral spine and from the neural spine of the first caudal vertebra.

INSERTION: Via a fascial sheet on the anterior surface of the tibial crest, just distal to the insertion of M. semitendinosus I.

REMARKS: This muscle has the same general form in the 11 study taxa.

M. semimembranosus (fig. 15)

ORIGIN: From the dorsolateral surface of the posterior half of the descending ramus of the pubis.

INSERTION: On the medial surface of the proximal tibia, deep to M. gracilis.

REMARKS: This muscle has the same general form in the 11 study taxa.

M. biceps femoris (fig. 14)

ORIGIN: From the ischial tuberosity and from the descending ramus of the pubis.

INSERTION: In fascia over the lateral side of the shank, from the falciform process of the tibia to the Achilles tendon.

REMARKS: This muscle has the same general form in the 11 study taxa.

Flexor Group of Leg

M. gastrocnemius (figs. 16–18)

ORIGIN: A medial head from a small fossa in the posterior surface of the medial epicondyle of the femur, and a lateral head from the posterior surface of the lateral epicondyle of the femur, where it is fused with M. plantaris.

INSERTION: The two heads join with the tendon of M. soleus to form the Achilles tendon, which inserts on the calcaneus.

REMARKS: This muscle has the same general form in the 11 study taxa.

M. plantaris (figs. 16 and 18)

ORIGIN: From the posterior surface of the lateral epicondyle of the femur, where it is fused with the lateral head of M. gastrocnemius.

INSERTION: Via a tendon that covers the posterior surface of the calcaneus and extends out the sole of the foot to form three branches. These branches extend out along the ventral surfaces of digits II, III, and IV and attach on the posterior margins of the proximal and middle phalanges.

REMARKS: This muscle has the same general form in the 11 study taxa.

M. soleus (fig. 17)

ORIGIN: From the dorsal and posterior surfaces of the posterior process of the fibula.

INSERTION: Via a tendon that contributes to the Achilles tendon and inserts on the calcaneus (see M. gastrocnemius).

REMARKS: This muscle has the same general form in the 11 study taxa.

M. popliteus (fig. 18)

ORIGIN: As a tendon from a pit on the posteroventral surface of the lateral epicondyle of the femur.

INSERTION: On the posterior crest of the tibia, proximal to the fusion of the tibia and fibula.

REMARKS: This muscle has the same general form in *Condylura*, *Desmana*, *Galemys*, *Neurotrichus*, *Parascalops*, *Scalopus*, *Scapanus*, *Scaptonyx*, *Talpa*, and *Urotrichus*. *Uropsilus* is similar except that the origin is from a sesamoid that lies adjacent to the lateral epicondyle.

M. flexor digitorum tibialis (fig. 18)

ORIGIN: From the posterior surface of the medial condyle of the tibia.

INSERTION: Via a tendon that attaches to the ventromedial surface of the medial tarsale, and then continues out into the sole of the foot.

REMARKS: This muscle has the same general form in *Condylura*, *Desmana*, *Neurotrichus*, *Parascalops*, *Scalopus*, *Scapanus*, *Scaptonyx*, *Talpa*, *Uropsilus*, and *Urotrichus*. In *Galemys*, this muscle originates as above, but apparently inserts just in connective tissue on the medial side of the foot, as I did not find a medial tarsale in this genus. See Reed (1951: 581) for a discussion of the medial tarsale.

M. tibialis posticus (fig. 18)

ORIGIN: From the medial surface of the posterior process of the fibula.

INSERTION: Via a tendon onto the posteromedial surface of the centrale.

REMARKS: This muscle has the same general form in *Condylura*, *Parascalops*, *Scalopus*, *Scapanus*, and *Urotrichus*. *Neurotrichus*, *Scaptonyx*, and *Uropsilus* are similar except that the insertion is on tarsale I. In *Desmana* and *Galemys*, this muscle originates as described above, but the muscle is quite small, and I could not trace its tendon. Dobson (1882–1890) stated that in these two genera the tendon of this muscle joins the tendon of M. flexor digitorum tibialis. M. tibialis posticus is apparently absent in *Talpa*. Reed (1951) reported that this muscle inserts on tarsale I in occasional specimens of *Scapanus*, so there may be variation in the insertion of this muscle.

M. flexor digitorum fibularis (figs. 17 and 18)

ORIGIN: A lateral head from the posterior surface of the posterior process and shaft of the fibula, and a medial head from the posterior and medial surfaces of the proximal tibia, the interosseus membrane, and the surfaces of the tibia and fibula adjacent to the interosseus membrane. These heads are fused for much of their length, and they form a single tendon.

INSERTION: Via a massive tendon that wraps around the medial side of the calcaneus and forms five branches that extend out the digits and attach to the ventral surfaces of the distal phalanges.

REMARKS: This muscle has the same general form in *Condylura*, *Desmana*, *Galemys*, *Parascalops*, *Scalopus*, *Scapanus*, *Talpa*, and *Uropsilus*. In *Neurotrichus*, *Scaptonyx*, and

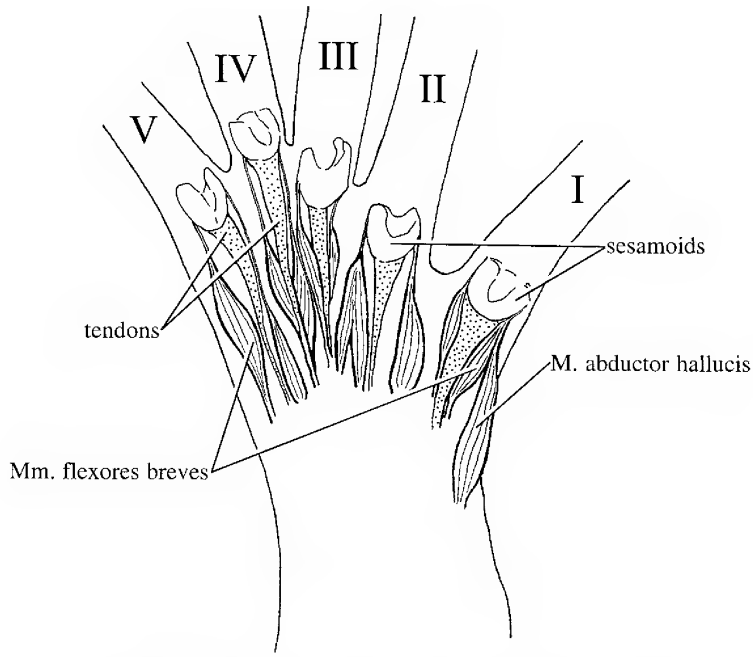

Fig. 19. Intrinsic muscles of the pes of *Neurotrichus*.

Urotrichus, the origin and insertion are similar, but the muscular heads are not fused, and the tendons remain separate until the distal end of the shank.

Flexor Group of the Pes

M. abductor hallucis (fig. 19)

ORIGIN: From a ridge on the plantar surface of the centrale.

INSERTION: Via a long tendon on the medial surface of the sesamoid that covers the metatarso-phalangeal joint of digit I.

REMARKS: I found this muscle in all of the study taxa except *Condylura*, *Desmana*, *Galemys*, *Talpa*, and *Uropsilus*. The homology of this muscle is unclear, and I follow Reed (1951) in using this name for it. Reed (1951) incorrectly claimed that it increases in size with increasing fossorial activity: it is well developed in *Scapanus*, but not in *Parascalops* or *Scalopus*, and it is apparently absent in *Talpa*.

Mm. flexores breves (fig. 19)

In *Uropsilus*, there is a medial and a lateral M. flexor brevis for each digit. The muscles for digits I and V originate from tiny sesamoids at the proximal ends of their respective metatarsals, whereas the muscles for the other digits originate from connective tissue over the tarso-metatarsal joints. Insertion is on paired sesamoids that lie on either side of the plantar surfaces of the metatarso-phalangeal joints. *Neurotrichus*, *Scaptonyx*, and *Urotrichus* also have paired muscles for each digit. These muscles originate from the proximal ends of the metatarsals and from connective tissue over the tarso-metatarsal joints, and they insert on the sides of the metatarso-phalangeal sesamoids. In these genera, and in all talpids other than *Uropsilus*, the metatarso-phalangeal sesamoids are single, and the flexor muscles insert on their respective sides of the sesamoid. *Desmana* and *Galemys* are similar to *Uropsilus* except that the medial flexor for digit I originates from the proximal end of the first metatarsal, and the lateral flexor for this digit is absent. In the remaining taxa there are fewer of these muscles. They originate from connective tissue at the base of the metatarsals, and the tendons of insertion continue past the metatarso-phalangeal sesamoids and wrap around the

sides of the digits to insert on a sesamoid on the dorsal surface of the first phalanx. *Condylura* has paired muscles for digits II and III and a medial muscle for digit IV. *Parascalops* has paired muscles for digits II and III and medial muscles for digits IV and V. *Talpa* has paired muscles for digits II, III, and IV. *Scalopus* and *Scapanus* have paired muscles for digits II and III and a medial muscle for digit IV.

REMARKS: I could not determine if the tendons of insertion extended to the dorsal surface of the digits in *Desmana*, *Galemys*, *Neurotrichus*, *Scaptonyx*, and *Urotrichus*. Also, there may be intraspecific variability in these muscles, as one of the specimens of *Scapanus* that I dissected also had a lateral muscle for digit IV and a medial muscle for digit V, and I could not find the medial muscle for digit V in some specimens of *Parascalops*. However, these are tiny muscles, and observational error or nongenetic factors (such as method of preservation or condition of specimens at the time of preservation) could explain the variability. Reed (1951) reported that *Neurotrichus* had three Mm. flexores breves per digit, but I believe that he confused a tendon that extends from the plantar connective tissue to the metatarso-phalangeal sesamoid of each digit for a third M. flexor brevis.

PHYLOGENETIC ANALYSIS

METHODS

Approximately 60 of the muscles described above exhibit significant intergeneric variation, and these were evaluated for use as characters. Twelve muscles were excluded, either because I was not confident that I had accurately described the differences between taxa, or because I considered these differences to be of questionable phylogenetic significance. The excluded muscles were Mm. pterygopharyngeus, psoas minor, serratus anterior thoracis, triceps brachialis caput medialis, extensor digitorum communis, cutaneus maximus, flexor carpi radialis, abductor digiti quinti, extensor hallucis longus, popliteus, flexor digitorum tibialis, and flexores breves of the pes. I could not determine the homologies of the individual elements in the Mm. sterno-cleido-mastoideus/occipitalis complex, and therefore I considered this group of muscles to represent a single character. Mm. trapezius posticus and dorsocuticularis are closely associated at their origins, have the same innervation, and always vary together, which suggests nonindependence, and therefore I used only M. trapezius posticus as a character. Mm. latissimus dorsi, subscapularis, extensor digiti quinti, extensor carpi ulnaris, and biceps brachii exhibit intergeneric variation at both origin and insertion, and because changes at the origin do not covary with changes at the insertion, I treated the origins and insertions as separate characters. Changes to the different heads of M. flexor digitorum profundus appear to be independent, and so I treated the heads as separate characters. Finally, I ordered the multistate characters for which I could hypothesize a logical relationship between character states (Lipscomb, 1992; Wilkinson, 1992). The result of this analysis was 58 myological characters, four of which were ordered.

Hypotheses of primary homology for the character states were made on the basis of topographic position and similarity of innervation (Wiley, 1981; Patterson, 1982; de Pinna, 1991). I dissected specimens of *Blarina* (Soricidae) and *Atelerix* (Erinaceidae) (table 2) to determine outgroup states for each character. The data matrix (table 3) contained the 11 study taxa plus *Blarina* and *Atelerix*. I used the branch-and-bound algorithm of PAUP* (version 4.0b1 for the Macintosh; Swofford, 1998) for the parsimony analysis, and specified that the outgroup taxa were paraphyletic with respect to a monophyletic ingroup. The analysis was performed with the characters both unordered and ordered.

CHARACTERS

1. M. digastricus venter anterior, medial sheet: (0) absent; (1) present.
2. Ear pinna musculature: (0) well developed; (1) absent.
3. M. cervico-auricularis pars profundus, insertion: (0) on posteromedial edge of auditory meatus; (1) into skin over the forelimb.
4. M. mandibulo-auricularis: (0) well de-

TABLE 3
Data Matrix
Taxa listed to indicate hypothesized patterns of synapomorphy. Characters 23, 34, 39, and 43 are ordered. ? = missing data.

	Characters
	000000000011111111112222222222333333333344444444445555555555
Taxa	123456789012345678901234567890123456789012345678901234567890123456789012345678
Atelerix	000001?0000001?300010001100000001000000000?0000?0000000000
Blarina	000000000000000000000000000000000010000100000000000000000010
Uropsilus	000000100000000?000000000000000000000010010000000000000001000001
Desmana	110000200011000?000111100110010021111000010101100101010?01
Galemys	?100??2000110000000011110011001002111100001010111000101 0?01
Condylura	110030001000000000001011100101000221110000111011010010001 01
Neurotrichus	110000011120101001110120101011002211100001121110101100001 0
Scaptonyx	110000011120101001110120101011002211100001121110101100?010
Urotrichus	110000011120101001110120101011002211100001121110101100011 0
Parascalops	111000011030111110113110101111331110111122011010011001 00
Talpa	111121011030111110110131101111113311101111220120100010120 1
Scalopus	111211111030111210110131101011113301102111220121100010110 0
Scapanus	111211011030111210110131101011113311102111220120100010110 0

veloped, originating from angular process; (1) well developed, originating from auditory bulla; (2) reduced or absent.

5. M. zygomaticus minor, insertion: (0) along lateral margin of external naris; (1) into posterior surface of external naris; (2) into ventral surface of external naris; (3) tendon splits to insert in nasal rays.
6. M. digastricus venter posterior, stylohyal origin: (0) present; (1) absent.
7. M. stylohyoideus: (0) originating lateral to M. digastricus, crossing over it; (1) originating medial to M. digastricus, not crossing over it; (2) absent or indistinguishably fused to M. digastricus.
8. M. cricopharyngeus: (0) absent; (1) present.
9. M. trapezius anticus pars capitis: (0) present; (1) absent.
10. M. trapezius anticus pars cervicis, origin: (0) from dorsal midline of neck; (1) from dorsal midline of neck and occiput.
11. M. trapezius anticus pars cervicis, insertion: (0) on metacromion; (1) on metacromion, with some posterior fibers on vertebral border of scapula; (2) on metacromion, with a separate posterior slip on vertebral border of scapula; (3) greatly reduced, not reaching scapula.
12. M. trapezius posticus, origin: (0) from lumbar vertebrae; (1) from lumbar vertebrae and iliac crest.
13. Mm. sterno-cleido-mastoideus/occipitalis complex: (0) 3 elements; (1) 4 elements.
14. M. splenius, origin: (0) from nuchal ligament and raphe of M. rhomboideus posticus; (1) from nuchal ligament only.
15. M. serratus dorsalis anterior, insertion: (0) via three slips; (1) via two slips.
16. M. serratus ventralis cervicis, origin: (0) a separate posterior head from first rib; (1) continuous, extending to first costovertebral articulation; (2) continuous, extending to first two costovertebral articulations; (3) from cervical vertebrae only.
17. M. rhomboideus posticus: (0) entirely muscular; (1) part of muscle forming stout interscapular ligament.
18. M. rhomboideus posticus, origin: (0) from median raphe and vertebral neural spines; (1) from median raphe only.
19. M. atlantoscapularis anterior: (0) present; (1) absent.
20. M. atlantoscapularis posterior: (0) present; (1) absent.
21. M. latissimus dorsi, origin: (0) from thoracic and lumbar vertebrae; (1) from thoracic and lumbar vertebrae and from iliac crest.

22. M. latissimus dorsi, insertion: (0) on teres tubercle of humerus; (1) on surface of M. teres major.
23. M. teres major, origin: (0) from axillovertebral angle of scapula; (1) from lateral surface and vertebral border of scapula; (2) from surface of M. subscapularis and vertebral border of scapula; (3) from distinct teres fossa, surface of M. subscapularis, and whole vertebral border of scapula. Ordered.
24. M. subscapularis, origin: (0) as two heads; (1) as one head.
25. M. subscapularis, insertion: (0) via two tendons; (1) via one tendon.
26. Mm. acromiodeltoideus and cleidodeltoideus: (0) separate; (1) fused.
27. M. acromiodeltoideus, origin: (0) from acromion process of scapula; (1) from clavicle.
28. M. infraspinatus: (0) present; (1) absent.
29. M. triceps brachii, caput lateralis, deep layer: (0) absent; (1) present.
30. M. extensor digiti quinti, origin: (0) from lateral epicondyle; (1) from lateral epicondyle and proximal crest of olecranon.
31. M. extensor digiti quinti, insertion: (0) on digits IV and V; (1) on digit V only.
32. M. extensor carpi ulnaris, origin: (0) from lateral epicondyle and olecranon; (1) from lateral epicondyle.
33. M. extensor carpi ulnaris, insertion: (0) on metacarpal V; (1) on sesamoid overlying metacarpal V; (2) on sesamoid overlying ulnare; (3) on second phalanx of digit IV.
34. M. subclavius: (0) 1 head inserting on clavicle; (1) 1 head inserting on clavicle and metacromion process; (2) 3 heads inserting on clavicle and metacromion process; (3) 3 heads inserting on clavicle and acromioclavicular ligament. Ordered.
35. M. pectoralis abdominalis: (0) absent; (1) present.
36. M. sternocuticularis: (0) absent; (1) present.
37. M. coracobrachialis: (0) absent; (1) present.
38. M. biceps brachii, origin: (0) as one head; (1) as two heads.
39. M. biceps brachii, insertion: (0) via one slip on proximal radius; (1) via one slip on middle of radius; (2) via two slips on middle of radius. Ordered.
40. M. epitrochleo-anconeus, origin: (0) as a single head; (1) as superficial and deep heads.
41. M. flexor carpi ulnaris, origin: (0) as two heads, from olecranon and from medial epicondyle; (1) as one head, from olecranon.
42. M. palmaris longus, tendon of insertion: (0) single, inserting in palm; (1) forked, inserting on digits I and V.
43. M. flexor digitorum superficialis, origin: (0) as three heads from humerus; (1) as two heads from humerus and one head from great flexor ligament; (2) as one head from humerus. Ordered.
44. M. flexor digitorum profundus, condyloulnaris head, insertion: (0) via separate tendon; (1) via tendon with ulnaris proprius head; (2) fleshily on flexor ligament.
45. M. flexor digitorum profundus, centralis head, origin: (0) from humerus; (1) from ulna.
46. M. flexor digitorum profundus, condyloradialis head: (0) muscular; (1) replaced by flexor ligament.
47. M. flexor digitorum profundus, radialis proprius head: (0) tendon separate to carpus; (1) inserting directly on main flexor tendon; (2) absent.
48. M. abductor pollicis brevis: (0) present; (1) absent.
49. Mm. flexores breves, manus: (0) present; (1) absent.
50. M. femorococcygeus, head from third trochanter: (0) absent; (1) present.
51. M. extensor digitorum longus, origin: (0) as a single head from lateral epicondyle; (1) as two heads, from lateral epicondyle and from fibula.
52. M. tibialis anticus, origin: (0) from tibia; (1) from tibia and lateral process of fibula.
53. M. peroneus digiti quarti: (0) present; (1) absent.
54. M. obturator internus: (0) present; (1) absent.
55. M. quadratus femoris, origin: (0) well posterior of acetabulum; (1) extending anteriorly as far as acetabulum.

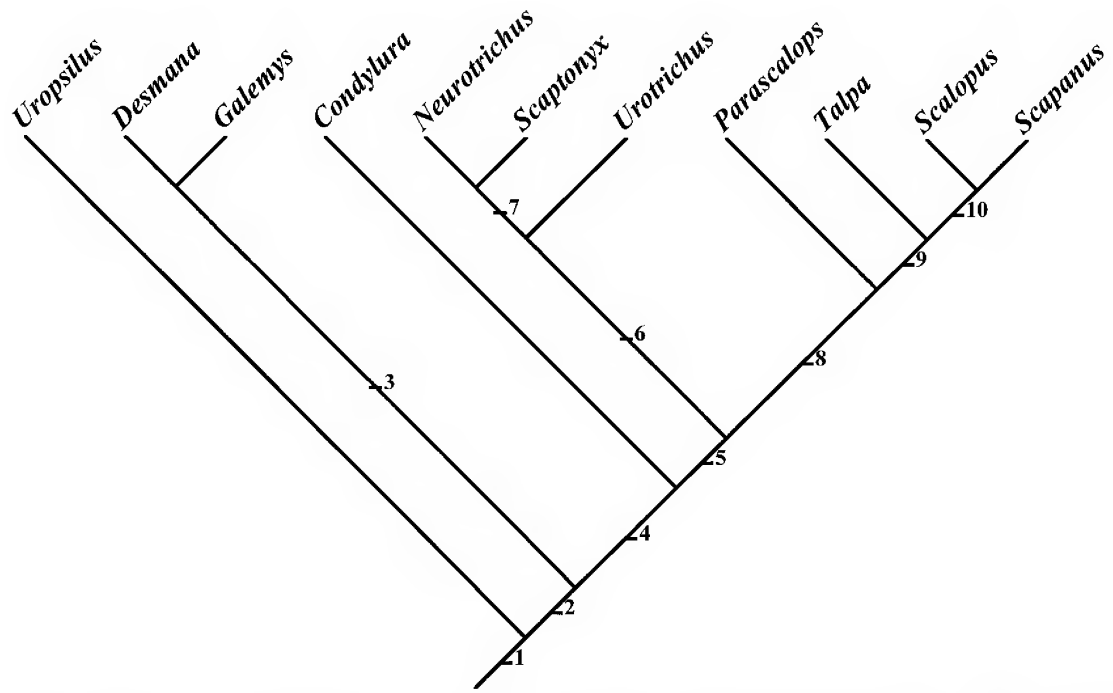

Fig. 20. Most parsimonious cladogram for the 58 myological characters (CI = 0.82, RI = 0.90). Numbers identify clades, which are discussed in the text and used in the apomorphy list (table 4).

56. M. tibialis posticus, insertion: (0) on tarsale I; (1) on centrale; (2) absent.
57. M. flexor digitorum fibularis, medial and lateral heads: (0) forming a single tendon; (1) forming tendons that remain separate to the tarsus.
58. M. abductor hallucis: (0) present; (1) absent.

RESULTS

The PAUP analysis with unordered characters discovered a single most parsimonious tree (fig. 20; apomorphy list table 4). This tree has a length of 94, a consistency index of 0.82, and a retention index of 0.90. Ordering of characters 23, 34, 39, and 43 did not affect the tree topology and did not change the tree statistics.

It was not possible to combine my dataset with other datasets because previous studies of talpid phylogeny have not published data matrices. However, I used MacClade (version 3.04; Maddison and Maddison, 1992) to constrain tree topology to the trees of Hutchison (1976) and Yates and Moore (1990). These other schemes of relationships provide much less parsimonious interpretations of the myological data: Hutchison's tree (fig. 1a) requires 30 additional steps (CI = 0.62, RI = 0.71), and Yates and Moore's tree (fig. 1b) requires a minimum of 33 additional steps (CI $\leq$ 0.61, RI $\leq$ 0.69).

DISCUSSION

SYSTEMATICS

The most parsimonious cladogram for the 58 myological characters (fig. 20) differs significantly from previous hypotheses of talpid relationships (fig. 1). Here I assess the support for the clades identified by this phylogenetic analysis, and I compare these clades with the groupings recognized in previous studies.

Clade 1: The present analysis discovered three unambiguous synapomorphies supporting the monophyly of the Talpidae: 35.1, 52.1, and 58.1. However, this analysis was

TABLE 4
Apomorphy List
Generated for most parsimonious cladogram (fig. 20). Includes only unambiguous changes.
* = unambiguous only when ordered.

Clade	Character	CI	Change
1	35. M. pectoralis abdominalis	0.500	0→1
	52. M. tibialis anticus	0.500	0→1
	58. M. abductor hallucis	0.333	0→1
Uropsilus	7. M. stylohyoideus	0.667	0→1
	38. M. biceps brachii, origin	1.000	0→1
2	1. M. digastricus, venter anterior	1.000	0→1
	2. Ear pinna musculature	1.000	0→1
	22. M. latissimus dorsi, insertion	1.000	0→1
	23. M. teres major	1.000	0→1
	27. M. acromiodeltoideus	1.000	0→1
	33. M. extensor carpi ulnaris, insertion	1.000	0→2
	34. M. subclavius*	1.000	0→1
	36. M. sternocuticularis	1.000	0→1
	42. M. palmaris longus	1.000	0→1
	44. M. flexor digitorum profundus, condylo-ulnaris	1.000	0→1
	46. M. flexor digitorum profundus, condylo-radialis	1.000	0→1
	47. M. flexor digitorum profundus, radialis proprius	1.000	0→1
3	7. M. stylohyoideus	0.667	0→2
	11. M. trapezius anticus cervicis, insertion	1.000	0→1
	12. M. trapezius posticus	1.000	0→1
	21. M. latissimus dorsi, origin	1.000	0→1
	26. Mm. acromiodeltoideus/cleidodeltoideus	1.000	0→1
	54. M. obturator internus	1.000	0→1
Desmana	50. M. femorococcygeus	1.000	0→1
Galemys	48. M. abductor pollicis brevis	0.500	0→1
4	9. M. trapezius anticus, pars capitis	1.000	0→1
	29. M. triceps brachialis, caput lateralis	1.000	0→1
	34. M. subclavius*	1.000	1→2
	43. M. flexor digitorum superficialis	1.000	0→1
	49. Mm. flexores breves, manus	1.000	0→1
Condylura	5. M. zygomaticus minor	1.000	0→3
5	8. M. cricopharyngeus	1.000	0→1
	13. M. sterno-cleido-mastoideus/occipitalis	1.000	0→1
	15. M. serratus dorsalis anterior	1.000	0→1
	19. M. atlantoscapularis anterior	1.000	0→1
	23. M. teres major*	1.000	1→2
	25. M. subscapularis, insertion	0.500	0→1
	44. M. flexor digitorum profundus, condylo-ulnaris	1.000	1→2
	58. M. abductor hallucis	0.333	1→0
6	10. M. trapezius anticus, pars cervicis, origin	1.000	0→1
	18. M. rhomboideus posticus, origin	1.000	0→1
	45. M. flexor digitorum profundus, centralis	1.000	0→1
	51. M. extensor digitorum longus	1.000	0→1
	57. M. flexor digitorum fibularis	0.500	0→1
Urotrichus	No unambiguous changes		
7	56. M. tibialis posticus	0.667	1→0

TABLE 4
(Continued)

Clade	Character	CI	Change
Neurotrichus	No unambiguous changes		
Scaptonyx	No unambiguous changes		
8	3. M. cervicoscapularis	1.000	0→1
	14. M. splenius	0.500	0→1
	16. M. serratus ventralis cervicis	1.000	0→1
	17. M. rhomboideus posticus, interscapular ligament	1.000	0→1
	23. M. teres major*	1.000	2→3
	31. M. extensor digiti quinti, insertion	1.000	0→1
	32. M. extensor carpi ulnaris, origin	0.500	0→1
	33. M. extensor carpi ulnaris, insertion	1.000	2→3
	34. M. subclavius	1.000	2→3
	39. M. biceps brachii, insertion	1.000	0→1
	40. M. epitrochleo-anconeus	1.000	0→1
	41. M. flexor carpi ulnaris	1.000	0→1
	43. M. flexor digitorum superficialis	1.000	1→2
	53. M. peroneus digiti quarti	1.000	0→1
Parascalops	No unambiguous changes		
9	6. M. digastricus, venter posterior	0.500	0→1
	47. M. flexor digitorum profundus, radialis proprius	1.000	1→2
	52. M. tibialis anticus	0.500	1→0
	55. M. quadratus femoris	1.000	0→1
Talpa	28. M. infraspinatus	1.000	0→1
	56. M. tibialis posticus	0.667	1→2
	58. M. abductor hallucis	0.333	0→1
10	16. M. serratus ventralis cervicis	1.000	1→2
	39. M. biceps brachii, insertion	1.000	1→2
Scalopus	7. M. stylohoideus	0.667	0→1
	35. M. pectoralis abdominalis	0.500	1→0
	48. M. abductor pollicis brevis	0.500	0→1
Scapanus	No unambiguous changes		

not designed to assess talpid monophyly, and it investigated only muscles that were variable within the study taxa. Proper evaluation of talpid monophyly would involve more complete dissections of outgroup taxa. The traditional placement of *Uropsilus* in the Talpidae has apparently been based largely or completely upon primitive characters. One possible osteological synapomorphy for the family is a humeroclavicular joint, a direct articulation between the lateral surface of the clavicle and the greater tuberosity of the humerus. Talpids other than *Uropsilus* have lost the normal mammalian acromioclavicular joint and have developed a humeroclavicular joint (Dobson, 1882–1890; Campbell, 1939; Reed, 1951). *Uropsilus* definitely retains a normal acromioclavicular joint (Campbell, 1939; Whidden, 1992), but it is unclear whether it also has a humeroclavicular joint. Dobson (1882–1890) and Campbell (1939) reported that *Uropsilus* has a partial humeroclavicular joint, but C. A. Reed (cited in Hutchison, 1976: 24) claimed that it has a typical mammalian shoulder girdle, with no humeroclavicular joint. My own dissections were inconclusive on this point.

Clade 2: This clade, which includes all talpids other than *Uropsilus*, is very strongly supported, with 12 unambiguous synapomor-

phies: 1.1, 2.1, 22.1, 23.1, 27.1, 33.2, 34.1, 36.1, 42.1, 44.1, 46.1, and 47.1. In addition, this clade has the complete development of a humeroclavicular articulation (Campbell, 1939; personal obs.).

Clade 3: Sister-taxon status for the two desmans has been generally recognized, and is supported by six unambiguous synapomorphies: 7.2, 11.1, 12.1, 21.1, 26.1, and 54.1.

Clade 4: This clade groups the aquatic/fossorial *Condylura* with the semifossorial *Neurotrichus*, *Scaptonyx*, and *Urotrichus* plus the fully fossorial *Parascalops*, *Talpa*, *Scalopus*, and *Scapanus*. The clade is well supported, with five unambiguous synapomorphies: 9.1, 29.1, 34.2, 43.1, and 49.1.

Clade 5: This clade links the semifossorial *Neurotrichus*, *Scaptonyx*, and *Urotrichus* with the fully fossorial *Parascalops*, *Talpa*, *Scalopus*, and *Scapanus*. Although this clade was not recognized by either Hutchison (1976) or Yates and Moore (1990), it is very well supported, with eight unambiguous synapomorphies: 8.1, 13.1, 15.1, 19.1, 23.2, 25.1, 44.2, and 58.0.

Clade 6: This clade groups the shrew moles *Neurotrichus* and *Urotrichus* with the long-tailed mole *Scaptonyx*. It is supported by five unambiguous synapomorphies: 10.1, 18.1, 45.1, 51.1, and 57.1. Despite the great similarity in the external form of these three genera, recent classifications (Van Valen, 1967; McKenna and Bell, 1997) and phylogenies (Hutchison, 1976; Yates and Moore, 1990) have separated *Scaptonyx* from *Neurotrichus* and *Urotrichus*. Van Valen (1967) used the relatively unspecialized dentition of *Scaptonyx* to justify this separation, and Ziegler (1971) claimed that tooth loss patterns made it extremely unlikely that these three genera are closely related to one another. However, tooth loss has occurred repeatedly in moles, and Nowak (1991) held that variation in tooth number is of little value in their classification. Yates and Moore (1990) listed three genic characters (presumably allozyme electromorphs) as uniting *Neurotrichus* and *Urotrichus* with the New World fossorial moles, to the exclusion of *Scaptonyx*, but they did not identify these characters.

Clade 7: Sister-taxon status for *Neurotrichus* and *Scaptonyx* is supported by one unambiguous synapomorphy, 56.0, a reversal.

Clade 8: A clade uniting the four fully fossorial genera (*Parascalops*, *Talpa*, *Scalopus*, and *Scapanus*) is very strongly supported, with 14 unambiguous synapomorphies: 3.1, 14.1, 16.1, 17.1, 23.3, 31.1, 32.1, 33.3, 34.3, 39.1, 40.1, 41.1, 43.2, and 53.1. Despite the strength of this support, neither Hutchison (1976) nor Yates and Moore (1990) considered the fully fossorial moles to be monophyletic (fig. 1). As noted earlier, I was not able to dissect *Scapanulus*, the Kansu mole from central China, but external form suggests that it is a member of this clade. Hutchison (1968) reported that *Parascalops* and *Scapanulus* are the only talpids with tetrahedral heterotopic bones between the clavicles and the manubrium, and these may be a synapomorphy uniting *Parascalops* and *Scapanulus* as sister taxa.

Clade 9: This clade links the Old World *Talpa* with the New World *Scalopus* and *Scapanus*. It is supported by four unambiguous myological synapomorphies: 6.1, 47.2, 52.0, and 55.1. Two derived basicranial characters provide further support: expansion of the ectotympanic to form a complete auditory bulla, and pneumatization of the basisphenoid region (personal obs.). Neither Hutchison (1976) nor Yates and Moore (1990) recognized this clade, but I consider it to be very well supported by the combination of myological and basicranial characters.

Clade 10: Sister-taxon status for *Scalopus* and *Scapanus* has been generally recognized, and is supported by two unambiguous synapomorphies: 16.2 and 39.2.

Biogeographic History

Comprehensive treatment of the biogeographic history of the Talpidae will require a phylogenetic analysis that includes the numerous described fossil talpids. However, the present phylogenetic analysis can be combined with information on recent (table 1) and fossil distributions of the extant taxa to make some inferences about talpid biogeography. The oldest fossils assigned to the Talpidae (*Eotalpa*, *Geotrypus*, and *Myxomygale*) are all from the late Eocene of Europe (Mc-

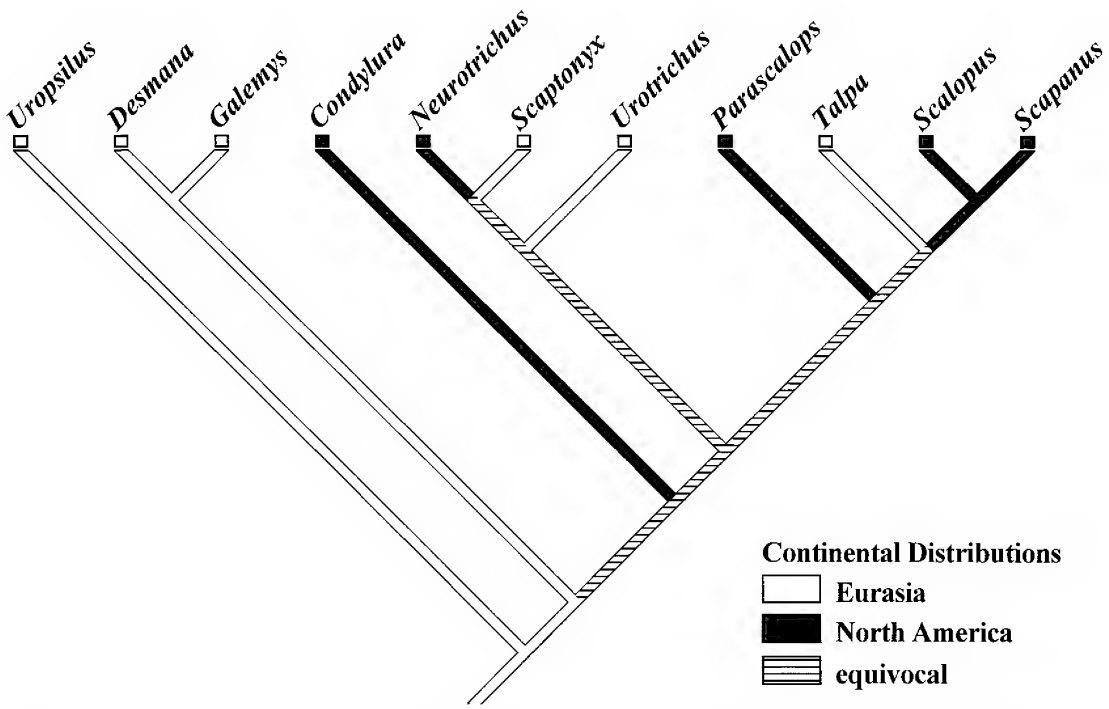

Fig. 21. Present continental distributions mapped on most parsimonious cladogram. Distributions from Corbet and Hill (1991).

Kenna and Bell, 1997). In contrast, talpids do not appear in Asia until the Oligocene and in North America until the late Oligocene (McKenna and Bell, 1997). These time differences suggest an origin for the group in Eurasia. They also suggest that the present-day North American mole fauna was derived through dispersal from Eurasia.

The paleogeographic evidence is consistent with this interpretation. Europe was apparently an island in the late Eocene when talpids first appear in the fossil record: the North Atlantic land bridges that connected Europe and North America in the early Tertiary had begun to break up by the early Eocene, and the Turgai Strait (Obik Sea) still separated Europe from Asia (McKenna, 1975, 1983b). The Turgai Strait was drying up by the end of the Eocene, and there is evidence of extensive faunal exchange between Asia and Europe in the early Oligocene (McKenna, 1983b), just when talpids appear in Asia. Dispersal between Eurasia and North America could have occurred across remnants of a North Atlantic connection, parts of which may have persisted until the Miocene (McKenna, 1983a, 1983b), but more likely it took place across a Bering land bridge, which apparently connected eastern Asia and western North America for most or all of the Tertiary (McKenna, 1975, 1983b).

Mapping the present continental distributions of the study taxa on the most parsimonious cladogram supports a Eurasian origin for the group (fig. 21). It also implies at least four dispersal events between Eurasia and North America. Although the mapping is ambiguous on the direction of the dispersals and on the taxa involved, the known fossil distributions of the extant taxa favor certain interpretations. *Condylura* is presently restricted to eastern North America, but it has been reported from the Pliocene of eastern Europe (Skoczen, 1993). This suggests an origin in Eurasia, dispersal to North America, and then subsequent extinction in Eurasia. *Neurotrichus* is presently restricted to western North America, but it has also been reported from the Pliocene of eastern Europe (Skoczen, 1993). The related *Scaptonyx* and

Urotrichus are known only from Eurasia (McKenna and Bell, 1997). These distributions suggest that this shrew-mole clade (fig. 20, clade 6) is essentially Eurasian, and that the occurrence of *Neurotrichus* in western North America is due to dispersal across Beringia, possibly as recently as the Pleistocene or Recent. Finally, monophyly of the fossorial moles (fig. 20, clade 8) implies at least one dispersal event between Eurasia and North America by a fully fossorial taxon. *Parascalops* is presently found only in eastern North America, but it has been reported from the Pliocene of eastern Europe (Skoczen, 1993). In contrast, *Talpa* is known only from Eurasia, and *Scalopus* and *Scapanus* are known only from North America (McKenna and Bell, 1997). These distributions suggest independent dispersals from Eurasia to North America by *Parascalops* and by the common ancestor of *Scalopus* and *Scapanus*.

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